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ROBERT LARSSON,
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THE PLANT SPECIES IN RELATION TO HABITAT AND CLIMATE

CONTRIBUTIONS TO THE KNOWLEDGE OF GENECOLOGICAL UNITS

BY *GÖTE TURESSON*
INSTITUTE OF GENETICS, ÅKARP, SWEDEN

IN a previous paper (TURESSON 1922) I endeavoured to show that the mass of genetically different biotypes which make up the Linnean species do not distribute themselves indiscriminately over an area comprising different types of localities. The biotypes, on the contrary, are found in nature to be grouped into different types, each confined to a definite habitat. I also produced facts which went to show that these habitat types, or *ecotypes* in my own terminology, do not originate through sporadic variation preserved by chance isolation; they are, on the contrary, to be considered as products arising through the sorting and controlling effect of the habitat factors upon the heterogeneous species-population. In the further consideration of these findings special attention was paid to the bearing upon the species problem and systematism which these studies implied, as well as upon ecology. The latter point was further developed in a subsequent publication (TURESSON 1923), where the importance of the distinction between modifications and hereditary variations in the field of ecology was emphasised, and the foundation of a new line of ecologic inquiry, viz. *genecology,* was proposed.

The material dealt with in my previous publications on this topic comprised mainly different species of the genus *Atriplex, Sedum maximum* (L.) SUTER, *Armeria vulgaris* WILLD., and *Hieracium umbellatum* L. It is my object in the following pages to present additional material in support of the conclusions already arrived at, as well as to raise some new problems which have become worth noting during the progress of the investigation. I shall also have occasion to discuss certain points in the works of some of those investigators who have in some way or other made use of the results set forth in my previous publications, e. g. CLAUSEN (1922), DU RIETZ (1923), HALL and CLEMENTS (1923), and HAUCH (1924).

A few introductory words should be said as to the material and cultures employed in this work. As stated before (TURESSON 1922) species with extended and uninterrupted distribution through regions climatically and edaphically dissimilar are best suited for investigations of this kind. Such species have thus been most extensively employed. The number of transplants made from various regions of such species and now in culture in the experimental fields of this Institute exceeds 10000. As regards methods of collecting and cultivating reference should be made to the paper cited above. Besides the cultivation on a large scale and under the same conditions of as many individuals as possible of different species breeding experiments are also in progress. It has not been thought wise, however, to postpone the publication of the work till these breeding experiments have been brought to an end as the evidence accumulated from the cultural experiments, as well as from the behaviour of the different types in their natural localities is sufficient to show the nature of the types dealt with in the following.

Before going further I wish to acknowledge my indebtedness to Professor H. NILSSON-EHLE for his generous efforts to provide necessary space at this Institute to the increasing mass of cultivated material. I also wish to express my deep gratitude to *Längmanska kulturfonden,* who has made it possible for me to collect material from such an extended area by granting me pecuniary support.

The photographs published in this paper have been taken by Messrs. K. B. KRISTOFFERSON and J. H. LEHMANN, to whom due acknowledgement is made.

I. MATERIAL AND CULTURES OF EDAPHIC AND CLIMATIC ECOTYPES.

For the sake of convenience the various ecotypes studied will be put together into their respective species. The grouping of the ecotypes distinguished within the different species will then be tried in connection with the general discussion of the results.

1. ECOTYPES OF ARTEMISIA CAMPESTRIS L.

It has been known for quite a long time that *Artemisia campestris* varies considerably in the field. From a systematic point of view the plant has been especially studied in our country by FRIES (1817, 1828) and by NEUMAN (1882). NEUMAN also gives some notes as

to the occurrence of the different forms in different habitats. My own cultures of the species include a number of series from various places in Scania and Öland: from the shifting dunes at Falsterbo and Löderup on the south coast of Sweden (in culture since 1920), from the salt meadows south of Cimbrishamn on the east coast of Scania (in culture since 1919), from dry pastures and gravelly fields at Sjöbo and Dalby in the interior of Scania (in culture since 1921) and from different places on calcareous rock (»Alfvar») on Öland, the island lying off the south-eastern coast of Sweden in the Baltic Sea (plants in culture since 1919 and 1922).

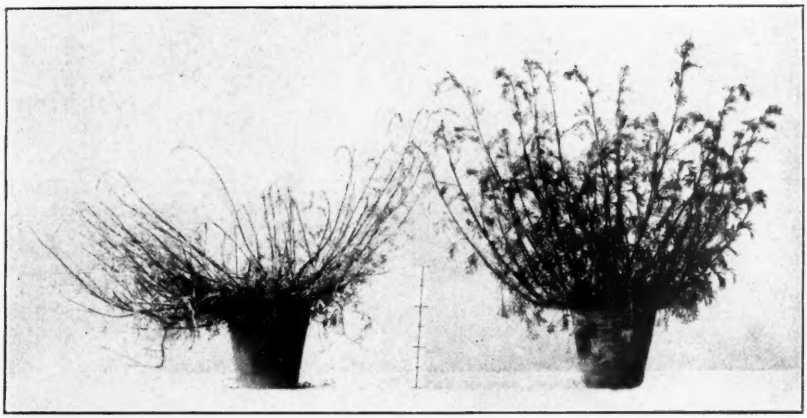

Fig. 1. *Artemisia campestris.* Cultivated individuals of the shifting dune type from Falsterbo. The measuring stick placed with the plants in this and the following photos measures 30 cm. in length.

The material from the shifting dunes is readily distinguished from the rest by its greyish-white hairiness, broader leaf segments, somewhat larger heads and a more upright habit of growth. It thus conforms fairly well with the variety *sericea* of FRIES, by NEUMAN (1901) treated as subspecies (see fig. 1).

The rest of my material would be classed as *campestris typica* by systematists. There is, however, a decided difference in growth form between the material from Scania and that from the calcareous rock formation on Öland. The former series include individuals with almost upright growth and those with almost horizontally expanded branches. Fig. 2 pictures the both extremes in the series brought home from Dalby, while fig. 3 shows the extreme growth

forms in the Sjöbo series. The majority of individuals lie between the extremes in both series. The cultivated series from Öland, however, do not contain any upright or ascending types; the indi-

Fig. 2. *Artemisia campestris.* Cult. individuals of the inland type from Dalby.

Fig. 3. *Artemisia campestris.* Cult. individuals of the inland type from Sjöbo.

viduals are all strongly plagiotropic, even more so than any of the plants in the Scanian series (see fig. 4).

That the more extreme habitat of the Öland plants also calls for more xerophytic structure is seen in the thickness of the outer wall of the upper epidermis (of the petiole) as compared with that of the

Scanian inland plants. While repeated measurements in different individuals of the latter series have given an average mean of 5 μ it has been found to be 7 μ in the Öland series. The remarkable thickness of the outer epidermis wall of *Artemisia campestris* from Öland has already been pointed out by GREVILLIUS (1896, p. 39) and by WITTE (1906, pp. 77—78), although their information pertains to »wild» and not to cultivated material. Any difference in wall thickness between the series in culture since 1919 and the one in culture since 1922 has not been found, which points in the direction of this character being of genotypical nature and not modificatory. That in the dune material the epidermis wall should also be of considerable thickness was to be expected. Measurements have given an average mean of even greater value than in the Öland plants, viz. 10 μ.

Fig. 4. *Artemisia campestris.* Cult. individual of the Alfvar type.

The hereditary nature of the dune type may be directly proven in the field, viz. in the regions where this type comes in contact with the ordinary type. Such zones, where both types more or less overlap, have been found in the south-eastern corner of Scania, where the dune region of Sandhammar meets the salt meadow fields to the north. No intermediate form is found in the neutral zone; a bewildering assemblage of forms which combine the characteristics of both types in different ways is met with instead. The same was found to hold true as regards different types of *Hieracium umbellatum,* as stated in a previous paper (TURESSON 1922, pp. 331—333), where views to the same effect, as those held by NÄGELI (1866) and BATESON (1913) are further developed.

There exists, moreover, a striking similarity in the habit of growth, on the one hand between the shifting dune types of *Hieracium umbellatum* and *Artemisia campestris,* on the other hand, between the stationary dune type of the former species and the Öland type of the latter species. The types of the mobile dunes are in both species ascending but not prostrate, while the types inhabiting stable ground although in other respects exposed to extreme conditions are extremely prostrate in both species.

The types of *Artemisia campestris* dealt with above thus group themselves into the following ecotypes:

a. The *dune ecotype* from the drift-sand and white dunes.
b. The *field and meadow ecotype* from the interior of Scania, as well as from the salt meadows along the coast.
c. The *Alfvar ecotype* from the calcareous fields and barren grounds on Öland.

2. ECOTYPES OF RUMEX ACETOSELLA L.

Samples of fruits of this species were obtained from calcareous localities on Öland (Vickleby) and were sown in 1920 together with

Fig. 5. *Rumex acetosella*. Cult. individuals of the ordinary inland type.

fruits of the same species collected in gravelly fields at Dalby (in the interior of Scania). Later on transplantations have also been made from different places on Öland (Vickleby and Askelunda) and Scania. The pygmaean form of this species from Öland has in all cases been found, upon culturing the plants, to be a mere habitat modification. The plants from Öland are, nevertheless, very different from those in the Scanian series. The latter are more or less erect and have rather broad leaves (fig. 5), while all the individuals of

the cultivated material from Öland are more or less prostrate and narrow-leafed (fig. 6).

The Öland type is sometimes distinguished as f. *angustifolius* KOCH, on account of its narrow leaves (WITTE 1906 a and b). The most striking characteristic, however, is the prostrate habit of growth, which is just as pronounced in the cultivated material as in the natural habitat. The results of the cultivations, especially those obtained from the sowing of fruits, strongly favour the opinion that the prostrateness of this type is a hereditary character and not a habitat modification.

It is thus seen that the Alfvar ecotype of *Rumex acetosella* repeats the growth form of the corresponding type of *Artemisia campestris,* viz. the prostrate habit of growth.

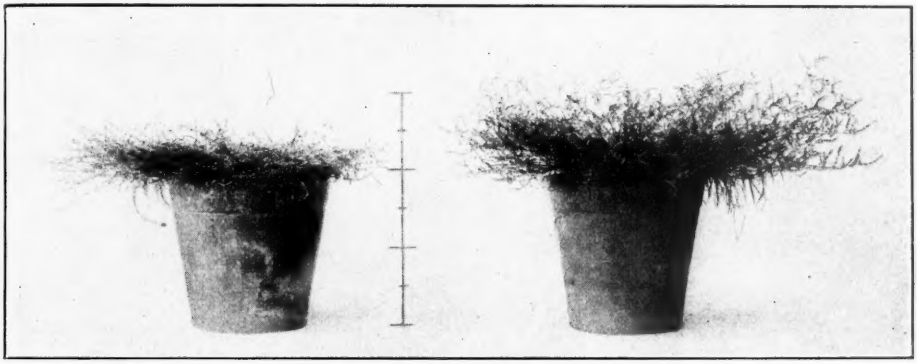

Fig. 6. *Rumex acetosella.* Cult. individuals of the Alfvar type.

3. ECOTYPES OF SILENE MARITIMA WITH.

A few specimens of this plant, collected on the Alfvar steppe on Öland as well as on the Swedish west coast (Lysekil), have been in my cultures since 1919. Larger collections of the same plant from Öland and the west coast were put in culture in 1922 and 1923.

The Alfvar type has been recognized as a special variety by systematists (v. *petræa* FR.), distinguished by the shape of the paracorolla, which in this variety is reduced to small protuberances. On account of the fact that the coast *maritima* also has sometimes a reduced paracorolla the validity of the variety is often doubted (cf. HARTMAN 1846, WITTE 1906 a, p. 45). Although the characteristic

in question, according to my own findings, must be said to hold true in the great majority of cases, there are distinguishing characters that are much more striking. The flowers of the Alfvar type are much smaller than in the coast type. This is also the case with the leaves. In addition, the stems of the Alfvar type are decidedly more procumbent than in the coast type. Figure 7, where the plant to the left shows the Alfvar type, the one to the right the coast type, as well as Table 1 (Alfvar type) and Table 2 (coast type) brings out these differences. The values of the length and width of petals and leaves

Fig. 7. *Silene maritima.* The plant on the left a cult. Alfvar plant, on the right a cult. individual of the coast type.

are average values from measurements made on 5 flowers and 5 leaves of each individual.

The young series would not have been tabulated were it not for the fact that the plants from similar habitats (4 from Öland, Resmo, 6 from Lysekil) cultivated since 1919 show exactly the same characteristics as those tabulated. There is thus little doubt as to the hereditary nature of the characters distinguishing the two types. This is also true of the prostrateness of the Öland type, which character becomes more and more marked as the plants grow older.

That the Alfvar type of *Silene maritima* is prostrate in its natural habitat has already been pointed out by ERIKSON (1895) and by WITTE (1906 b). That this growth form, however, is a here-

TABLE 1. *Silene maritima No. 644, Öland (Vickleby).* Plants in culture since 1923. Notes taken 1924.

Field number	Length of longest stem in mm.	Length of the petal limb	Width of the petal limb	Length of middle stem leaves	Width of middle stem leaves in the middle
1	280	4,08	2,43	29,4	5,46
2	375	4,34	2,36	30	5,2
3	250	5,22	2,96	24,6	3,56
4	260	5,12	2,1	16,8	2,22
5	225	4,12	2,32	21	3,78
6	320	5,02	2,97	18,2	4,2
7	290	4,32	2,58	19,2	4,8
8	285	4,48	3,23	22,8	4,58
9	280	4,76	3,09	23,6	5
10	315	5,52	2,81	22,6	4
11	260	5,4	2,87	20,8	3,44
12	260	5,94	3,00	21,8	3,76
13	310	4,94	2,86	23,82	5,8
14	310	3,76	2,47	26,62	4,4
15	270	4,96	2,8	26,22	4,36
16	340	4,76	2,92	28	4,62
17	220	4,56	2,52	17,24	3
18	300	4,88	2,68	21,62	3,38
19	245	4,9	3,25	22,8	5,4
20	250	3,92	2,42	24,22	3,78
21	280	6,48	3,47	23,8	4,4
22	255	5,46	3,21	27,22	4,22
23	280	4,92	2,8	21,4	4
24	250	4,28	3,05	20,02	4,42
25	315	5,06	3,6	22,44	4,42
26	330	5,18	3,56	20,8	3,62
27	330	5,32	3,05	21,8	3,8
28	320	4,96	3,47	23,4	3,64
29	350	5,1	2,72	24,82	4,02
30	300	4,88	2,64	22,82	4,18
Average in mm.	285,17	4,88	2,87	23	4,18

ditary feature and not a habitat modification now seems clear, and it illustrates at the same time the close agreement between the Alfvar ecotype of this species and those of *Artemisia campestris* and *Rumex acetosella.*

TABLE 2. *Silene maritima No. 761, Hallands Väderö.* Plants in culture since 1923. Notes taken 1924.

Field number	Length of longest stem in mm.	Length of the petal limb	Width of the petal limb	Length of middle stem leaves	Width of middle stem leaves in the middle
1	465	12,06	8,66	25,38	5,22
2	355	10,42	6,9	27,82	5
3	440	—	—	28,42	8,24
4	400	9,42	7,6	27,58	6,6
5	440	9,83	7,97	28,4	5,2
6	500	—	—	40,2	5,62
7	270	9,42	6,84	24,98	4,4
8	470	—	—	30,8	5,18
9	430	—	—	40,04	6,6
10	460	11,06	6,48	40,2	7,4
11	460	—	—	27,02	6,18
12	360	—	—	32,6	4,2
13	335	—	—	24,6	7,4
14	340	9,82	8,28	33,6	4,2
15	450	—	—	29,4	5,6
16	360	10,68	8,04	30,4	4,8
Average in mm.	408,44	10,33	7,59	30,72	5,74

4. ECOTYPES OF ALLIUM SCHOENOPRASUM L.

The cultivated material of this species comprises rather large series from the coast of Blekinge in Southern Sweden, from the rocky islets off Stockholm and from the calcareous Alfvar steppe on Öland. The material from the two first mentioned localities does not show any marked dissimilarities, while the Öland material represents an altogether different type. Fig. 8 shows the Öland type (to the left) and the coast type (to the right), both from series cultivated during two years. Awaiting the results of the crosses made between the two types clones were raised in 1924. The clone material brings out the differences in the same degree as the original transplants, which strongly favour the belief that the characteristics in question are hereditary and not modificatory.

The Öland type is lower in stature than the coast type, the leaves do not overreach the scapes in the former type as in the latter; they do not bend over as is the case in the coast type, which is on

the whole less robust than the Öland type. The leaves of this type are, moreover, glaucous, but pure green in the coast type. The colour of the flowers is deaper blue in the Öland type (although pure white-flowering plants sometimes occur on the Alfvar) while the colour is a lighter blue in the coast type. The flowering time is also different; the former flowers regularly 10—15 days earlier than the latter. The young clone material repeats, as said above, every one of the distinctive characters of the two types.

Fig. 8. *Allium Schoenoprasum.* The plant on the left a cult. Alfvar plant, on the right a cult. coast plant.

I refrain here from entering upon the complicated question of the spontaneousness of the coast type, as well as upon the question of the relationship of the types to *A. sibiricum* L. Extensive cultures with material from other regions are needed for the solution of these problems. The point emphasised here is the unquestionable genotypical differences between the coast type and the Öland type. That the latter is specialized for ecologically quite another kind of habitat than the former seems also certain. It is, no doubt, a regular Alfvar ecotype, with features typical of plants inhabiting exposed

and arid localities (reduced stature, reduced transpiration surfaces, glaucousness).

It is interesting to note that already LINNÆUS (1745, p. 53) has observed the habit of the ordinary type to bend the leaves contrary to the Alfvar type, which holds the leaves erect. He describes the

Fig. 9. *Lythrum salicaria.* The plant on the left a cult. individual of the coast type, on the right a cult. individual of the inland swamp type.

Alfvar plant brought home from Öland and planted in Upsala in the following way: »Denna planterade jag uti Upsala trägård, der han är så aldeles lik den ordinaria gräslöken, at ingen skillnad märkes utan det at Trägårds-gräslöken, då han först upspritter, har tilbakes bögda blad-spitsar, men denna intet så.» (»I planted this in the Upsala garden, where it is so similar to the ordinary Chive that no difference could be noted except that the Chive, when emerging, has

the leaf tips bent backwards, while they are not so in this»). With more extensive cultures at hand LINNÆUS would no doubt have noticed the additional differences between the two types.

5. COAST ECOTYPES OF INLAND SPECIES.

In a previous paper (TURESSON 1922) several instances were given of inland species with hereditary coast types (*Solanum Dulcamara* L., *Matricaria inodora* L., *Leontodon autumnalis* L.). Although

Fig. 10. *Plantago major.* The plant on the left a cult. individual of the inland type, on the right a cult. coast plant.

it is not my intention to enlarge upon the subject on this occasion, a few words might be said with regard to the occurrence of such coast types in other species, e. g. in *Lythrum salicaria* L. and *Plantago major* L. They are as yet insufficiently studied, although little doubt remains as to the hereditary nature of the forms in question.

In 1921 collections of *Lythrum salicaria* were made along the Swedish west coast (Arild in Scania and at Lysekil in Bohuslän) and these were cultivated along with material from inland swamps (Stehag in Scania). The coast material was collected in pools of brackish water. The variation within the series is small, while the

differences between the coast and the inland series are remarkable. Fig. 9 brings out some of these differences. The coast type (to the left) is stout and robust and lower in stature than the ordinary type (to the right; the drooping of the tips is due to wilting, which sets in much sooner in this type than in the coast type). The colour of the flower is a deeper red in the coast type, and the spikes are

TABLE 3. *Plantago major No. 404, Åkarp.*
Plants in culture since 1921. Notes taken 1924.

Field number	Length of longest scape in mm.	Length of leafblade	Width of leaves	Length of petiole	Length of spike	Length of spike-stalk
1	340	66,66	70	18	130	166,66
2	250	93,3	75	43,3	112,5	110
3	300	90	68,03	35	150	140
4	220	75	55	50	83,33	120
5	200	—	—	—	68	120,6
6	160	66,6	45	40	70	90
7	230	73	47	48	94	117,5
8	120	—	—	—	—	—
9	290	83	62,5	55	128	130
10	100	57,6	47	98,3	—	—
11	340	101,6	76	81,66	148,5	202,5
12	220	90	81	80	85	128
13	280	80	68	75	110	150
14	270	75	57	42	130	85
15	330	93,3	66,6	49,3	116,5	147,5
16	290	74	60	50,5	143	130
Average in mm.	246,2	79,93	62,72	54,72	112,06	131,27

thick and dense compared with those of the inland type. The leaves of the coast types are in addition shorter and thicker than those of the latter type.

The material of *Plantago major* includes cultivated inland series from different provinces in Sweden (Scania, Västergötland) as well as from Germany, and coast series from Arild and Värmdö (in the Stockholm archipelago). Although considerable variation is found in the inland series the greatest differences are found between these series and the coast series. Fig. 10 pictures representative individuals of the inland plants (from Åkarp, to the left) and of the coast plants

(from Värmdö, to the right). In tables 3 and 4, where the values of the length and width of leaves and the length of petioles and spike-stalks are average values of 5 different measurements of each individual, further information is given as to the distinctive characters. The long, narrow leaves, somewhat more fleshy than in the inland plant, and the great length of the spike-stalk are very characteristic

TABLE 4. *Plantago major No. 276, Värmdö.*
Plants in culture since 1919. Notes taken 1924.

Field number	Length of longest scape in mm.	Length of leafblade	Width of leaves	Length of petiole	Length of spike	Length of spike-stalk
1	610	150	77	188	227	324,1
2	600	161	98	180,4	241	320,4
3	420	148	73	144	124	261
4	500	144,1	75	154	204	306
5	390	115	63,1	142,1	164	229
6	420	145	77	173	146	288
7	400	114	85	137	157	252
8	430	140	77	142	170,5	242,1
9	550	152,1	61,2	157,1	169	335
10	490	68	39	114	181,1	321,1
11	630	134	64	144	210	298
12	400	146	72	160	134	212
13	670	166	84	194	282	298
14	420	154	80	190	166	286
15	450	116	80	158	155	272
16	470	120	78	146	170	230
Average in mm.	490,6	135,82	73,95	157,72	181,28	279,66

of the coast type. It is on the whole much more robust and bulky than the inland type and would, no doubt, attain gigantic dimensions in the cultures were it not for the attacks of powdery mildews which damage the coast plants far more than those of the inland type.

In its natural habitat, the lower supralittoral belt, the individuals of the coast type are of very much smaller size, and the distinctive characters are less conspicuous. However, the type in question no doubt represents the indigenous, »wild» type of *Plantago major*, which is at present found typically only in such places where no cultivated fields or roads run down to the shore line, or, in other words, where

bastardization with the anthropophytic inland types is excluded. The rareness of typical coast type individuals along our shores is otherwise hard to understand. The coast type of *Plantago major* is thus seen to behave much in the same way as the corresponding types of *Leontodon autumnalis* and *Matricaria inodora* (TURESSON 1922).

It should be added that the plant, as found in its natural habi-

Fig. 11. *Spiræa ulmaria.* Cult. individual of the coast type.

tat, matches fairly well the *scoparia* form of the systematists, while the same plant in the experimental fields at Åkarp falls outside the diagnosis given to this form.

6. ECOTYPES OF SPIRÆA ULMARIA L.

The cultures of this widely distributed species comprise series from the west coast (Arild and Lysekil, coll. 1921), inland series from the southern part of the country (Stehag and Krageholm in Scania, coll. 1920), as well as from the central Scandinavian mountain districts (Jämtland and Härjedalen, coll. 1921). Series of this

plant have also been brought in culture from the far North (Lappland), as well as from Germany and Austria but the treatment of these series will be postponed on account of the youth of the cultures.

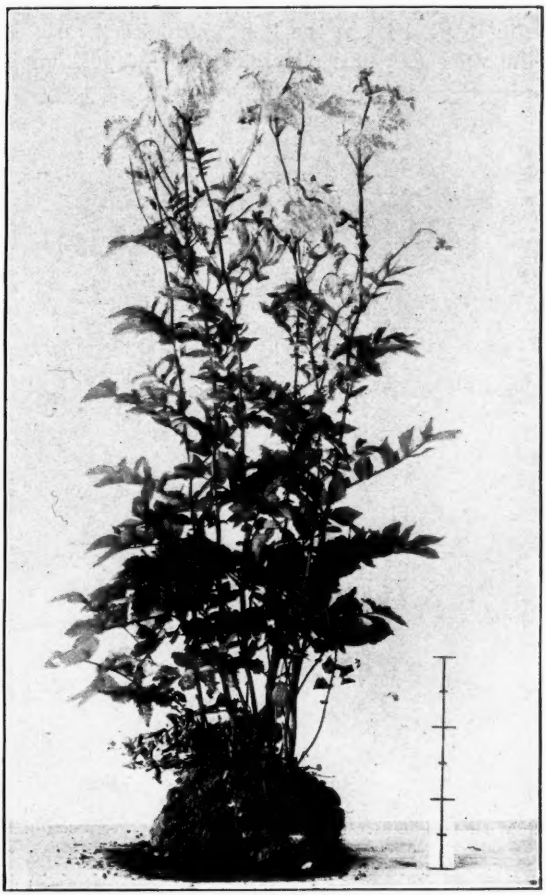

Fig. 12. *Spiræa ulmaria.* Cult. individual of the southern inland type.

When grŏwing side by side in the cultures striking differences are seen between the series from the different regions. The hereditary nature of these differences cannot be doubted when it is found that the characteristics typical of the plants in their respective

habitats become more and more marked in the cultures as the plants grow older. Apart from other pecularities to be dealt with below the coast type has in all cases been found to have curved leaves, while the inland type (cf. the coast type in fig. 11 and the southern inland type in fig. 12) keeps the leaves straight at an angle of about 60° from the vertical. This characteristic leaf position is less mar-

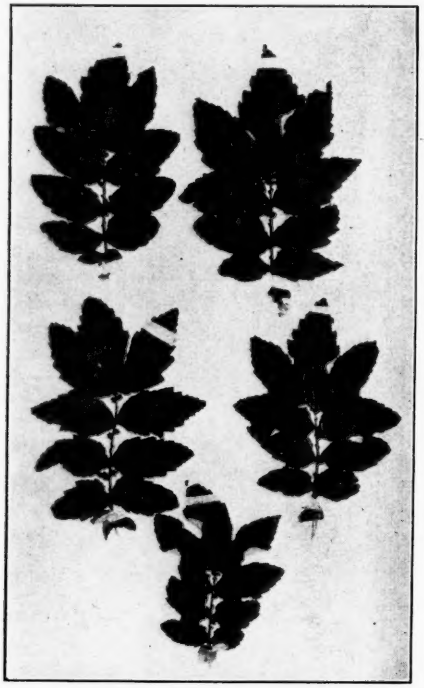

Fig. 13. *Spiræa ulmaria.* Dried and mounted middle stem leaves of the cult. type, from the central Scandinavian mountain district.

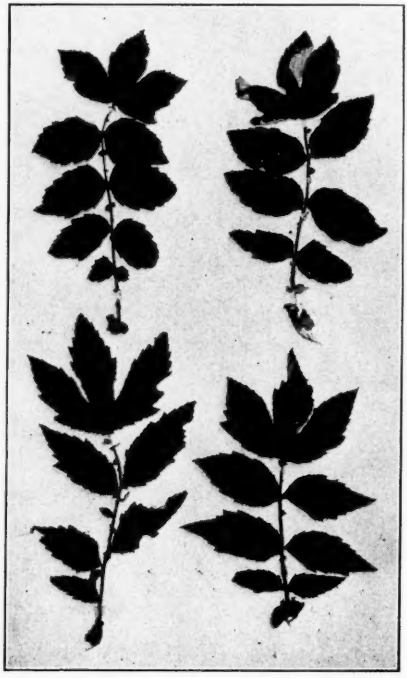

Fig. 14. *Spiræa ulmaria.* Dried and mounted middle stem leaves of the cult. southern inland type.

ked in the natural habitat but becomes very marked in the cultures. Similarly the »internodes» between the different pair of leaflets are decidedly shorter in the type from the central Scandinavian mountain districts than in the southern type (cf. figs. 13 and 14). This characteristic is not easily seen in the habitat, although noticeable, while under cultural conditions it is at once seen as soon as the plants become vigorous. The crowded position of the leaflets in the

northern type, when compared with the southern type, is also seen in tables 5, 6 a and 6, the data of which are based upon average values derived from measurements of 6 leaflets from each individual. The length of the »internode» refers to the distance between the second and third pair of leaflets counting the terminal leaflet as no. 1. Only leaves from the middle part of the stem are considered.

TABLE 5. *Spiræa ulmaria No. 169, Stehag.*
Plants in culture since 1920. Notes taken 1924.

Field number	Length of longest stem in mm.	Length of »internode»	Length of leaflet of the second pair	Width of leaflet of the second pair
1	800	20	43,5	21,8
2	1000	30,03	52,6	27,8
3	1040	27	59,3	28,3
4	950	30,3	53,1	27,3
5	700	17,6	39,5	17
6	850	24,3	49,1	21
7	1110	37,3	62,6	26,1
8	1120	23,1	46,8	25
9	1120	25	54,2	21,1
10	1000	23,3	42,1	25,1
11	770	24	50	34
12	790	20,3	45	27,6
13	900	25	48	28,5
14	900	21,6	49,1	24,3
15	800	31	49,1	27,1
16	110	34,04	57,1	25,1
Average in mm.	928,1	29,48	49,44	25,44

The coast type is on the whole lower in stature than the inland types. The average height of the two series, 26 individuals in all, amounts to 70 cm., while the average height of the inland series is about 90 cm. (see tables). There is, moreover, marked differences in the time of flowering between the different types. This is especially striking in the case of the southern and the northern types. The latter flowers about 10 days earlier than the former type. This difference is remarkably constant in successive years.

As to the anatomical structure of the leaves important differen-

TABLE 6. *Spiræa ulmaria No. 215, Åre, Jmtl.*
Plants in culture since 1921. Notes taken 1924.

Field number	Length of longest stem in mm.	Length of »internode»	Length of leaflet of the second pair	Width of leaflet of the second pair
1	820	15	56,2	30,4
2	790	24,5	47	21
3	700	25	49	27,2
4	680	18,3	54,2	24,5
5	780	17,5	56,1	26
6	1000	18,2	53	23,1
7	1020	20	48,2	26,03
8	1030	14,03	54,7	32,1
9	690	26,1	56,3	25
10	1010	16,03	60	26,5
11	1170	17,2	49,03	27,3
12	690	20,7	57	24
13	720	19,6	53,5	20
14	790	18,2	52,1	24,2
15	1000	15	53	23,1
Average in mm.	859,3	19,02	53,28	25,49

TABLE 6 a. *Spiræa ulmaria No. 217, Frösön, Jmtl.*
Plants in culture since 1921. Notes taken 1924.

1	670	18,7	46	27,8
2	700	17	54,1	26
3	800	18,1	57,1	24,1
4	810	20	55,1	29,1
5	1040	17,03	50	28,1
6	700	16	46,1	20
7	1020	19	56,1	30,5
8	1120	18,1	60,1	33,1
9	1070	27,1	57,1	26,1
10	1030	21,03	55,1	27,01
11	1050	26,13	53,1	27,1
12	1000	25	58,1	25
13	780	15	50,03	19,01
Average in mm.	906,9	19,86	53,69	26,31

ces are seen in the cultivated types. The leaf-thickness varies with the place of the leaves on the stem, as pointed out by YAPP (1912), and therefore care has been taken to compare leaves with the same relative position on the stem in the different types. The values given below are average values from a number of measurements made on terminal leaflets of middle stem leaves collected in the cultures in 1924. The leaf-thickness varies in the different types in the following way:

The coast type	The northern type	The southern type
140—165 μ	130 μ	80—95 μ

The differences in the leaf-thickness are not due to the varying number of palisade layers, (there are in general two layers in all three types) but especially to the different depths of the palisades and the spongy mesophyll in the types. Representative sections from the different types have given the following values (see also figs. 15 and 16):

	The coast type	The northern type	The southern type
(Outer epidermis wall) ..	5,4 μ	4,5 μ	4,5 μ
Upper epidermis	22,2	22,2	18,5
Palisades	70,3	59,2	44,4
Spongy mesophyll	51,8	40,7	18,5
Lower epidermis	11,1	11,1	11,1

It should also be mentioned that in the case of the coast type the leaf thickness has been found to increase under culture. When first brought in culture the thickness of the leaves were thought to be a habitat modification and measurements were made in order that the suspected retrogression to the inland type could be followed. The average leaf-thickness in the habitat amounted to 130—140 μ. With the increase in vigour made possible by the cultural conditions an increase in leaf-thickness has also followed, which goes to show that the leaf-thickness characteristic of the coast plants is a hereditary feature in the plants investigated and not a habitat modification.

The treatment of *Spiræa ulmaria* by systematists has resulted in a large number of forms and varieties generally based upon characters pertaining to differences in leaf shape and hairiness. The great majority of these systematic forms, however, is of no value for the grouping of the *ulmaria*-population in ecotypes. Within each series brought home from the different regions there are variations both in leaf shape, and in hairiness. The var. *denudata* (PRESL) BECK., for

instance, is present in all three types dealt with above. Quite other characteristics have to be considered when it comes to a grouping into ecotypes. In the present treatment of the question some of these characteristics have been dealt with, and a subsequent investigation, which aims at a more detailed description of the ecotype segregation of the species-population in different regions of its much extended area of distribution, will demonstrate this fact more clearly. I hope to have shown, however, that extensive cultures of material from widely different regions is needed before any understanding of the ecology of this species, as well as of other species can be obtained (cf. TURESSON 1923). When, therefore, YAPP (1912), in his most valuable paper on *Spiræa ulmaria*, calls his treatise an experiment in »species-ecology» the approximation to such an end is but slight. Without the consideration of the hereditary variations and characters found within the population, which enable the »species» to inhabit regions climatically so different as Lappland and southern Italy, an understanding of the ecology of the species will never be reached.

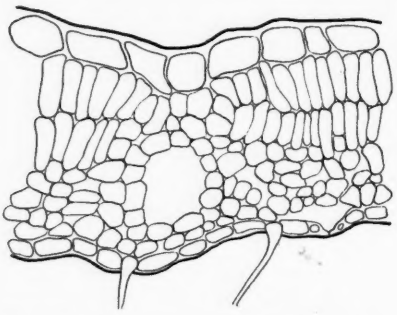

Fig. 15. Cross section of a middle stem leaf of a cult. coast type individual of *Spiræa ulmaria*. Drawn with a Zeiss camera lucida. × 190.

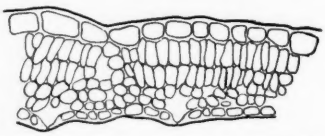

Fig. 16. Cross section of a middle stem leaf of a cult. southern inland type of *Spiræa ulmaria*. Drawn with a Zeiss camera lucida. × 190.

7. ECOTYPES OF SUCCISA PRATENSIS MOENCH.

Salt meadow types of this species as well as inland types from the southern part of the country have been dealt with in a previous paper (TURESSON 1922). Efforts have been made, however, to secure material from other regions as well. These series include material from the central Scandinavian mountain district (Jämtland) and Lappland. I have also series from Bodö on the west coast of Norway (north of the polar circle), as well as from Germany and Austria.

Most of the material, however, is too young to be considered at present. Part of the boreal material, viz. the three year old cultures from Jämtland (Åre) and the two year old cultures from Bodö, show even now interesting differences from the material collected in the south. There is especially one characteristic feature of the northern material, viz. the powerful development of the radical leaves, which is undoubtedly a hereditary feature, being now much more marked than in the first year of cultivation. It is not only that the radical

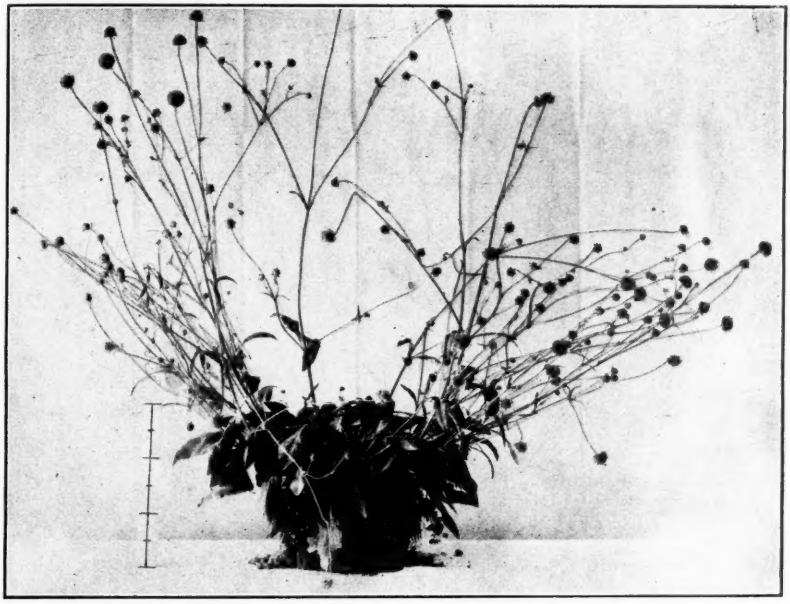

Fig. 17. *Succisa pratensis.* Cult. individual of the northern type.

leaves reach an unusual degree of development in this type, the cauline leaves too behave differently in this northern type. Because of the short internodes in the lower part of the stems they become much more collected at the base of the stem than in the southern types, thus increasing the mass of ground leaves. The northern type, therefore, has a large leaf cushion, while the southern types are less dense and tufted (cf. figs. 17 and 18).

Moreover, the northern type flowers about a week earlier than the southern types. The anatomical structure of the leaves differs

also in the different types. The thickness of the radical leaves, measured on cultivated material in 1924, is about 260 μ in the southern inland type, while in the boreal type it reaches about 300 μ. The number of palisade layers is the same, viz. two, and the increase in thickness is due to differences in the development of the spongy mesophyll.

Leaf cushion, early flowering and increased leaf thickness are all characters, which are ascribed to species inhabiting alpine or

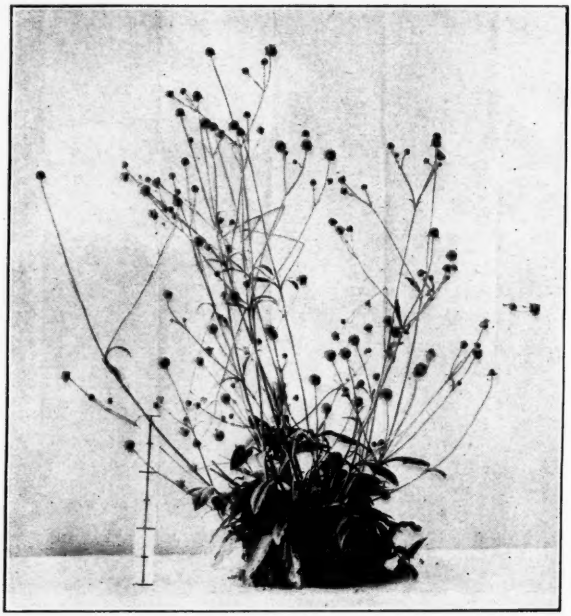

Fig. 18. *Succisa pratensis.* Cult. individual of the southern type.

arctic regions. When it is found that characteristics typical of notorious alpine species also characterize our northern material of *Succisa pratensis,* and when in addition it is shown that one of the most striking features, viz. the cushion growth, must be of a genotypical nature the conclusion seems warranted that the type in question represents the northern ecotype of the species.

8. ECOTYPES OF MYOSOTIS SILVATICA HOFFM.

Material of this species including var. *alpestris* KOCH (syn. *M. alpestris* SCHMIDT) has been collected and brought in culture from

lowland and alpine regions in Scandinavia, as well as from Germany, Austria and the Carpathians. The extra-Scandinavian material will not be considered at this time, as it is too young. Most of the Scandinavian series are readily grouped in two types, the lowland type and the mountain type, with exception of a few which undoubtedly show intermediate characters. Lowland series old enough to allow comparison are those brought home from Bökeberg in 1921 and from Stehag in 1920 (both localities in Scania). The typical mountain series are considerably younger, but clones have been made from a number of individuals of these series in order to secure a better material for comparison. These series include two year old cultures from Torne Träsk in Lappland and Dovre in Norway, and three year old cultures from Finse in the Hardanger district in Norway. The first series comes from the subalpine birch region of a type which is called »Kräuterreicher Wiesenbirkenwald» by FRIES (1913); the Dovre series is also subalpine, forming part of a vegetation type related to »Kräuterreiches Wiesenweidengebüsch» of FRIES. The Finse series comes from the alpine region at about 1350 m. sup. m.

Although the Scandinavian mountain type does not seem to be quite identical with the *M. alpestris* of the Alps (a subsequent paper will treat these interesting points more fully) considerable differences between the types are seen in the cultures. The lowland type is higher in stature than the mountain types. The average height of a series of 21 individuals from Bökeberg, measured in the cultures in 1924, was 396,5 mm., while the average of 18 cultivated individuals from Dovre, measured the same year, was 260,2 mm. The radical leaves of the mountain types are more rounded and have longer petioles than the lowland series. The calyx is also more hairy than in the lowland type. The power of leaf regeneration at the base is strong in the mountain types, but weak in the lowland type. The former takes the character of cushion plants. Fig. 19 brings out this character very clearly.

Again, there are interesting points of difference between the subalpine and the alpine material. The latter material does not attain the height of the former. The average height of the Finse plants is about 200 mm. This additional dwarfing in the alpine material repeats itself regularly in the clone series, which strengthens the view that genotypical differences are the causes of these height differences.

The anatomical structure of the leaf offers additional differences. The leaf thickness varies considerably in the types. The following values are average values from numerous measurements of cross-sections of radical leaves collected from the clone series in 1924.

The lowland type	The Dovre-Torne Träsk type	The Finse type
250 μ	380 μ	515 μ

Fig. 19. *Myosotis silvatica.* Cult. individuals of the subalpine type (on the left), and of the southern or lowland type (on the right).

In general, two palisade layers are found in all the types, and the differences found are due to the different depths especially of the palisades and the spongy mesophyll. Representative sections from the different types have given the following values (cf. figs. 20 and 21):

	The lowland type	The Dovre and Torne Träsk types		The Finse type
Upper epidermis	27,0 μ	29,3 μ	27,5 μ	31,5 μ
Palisades	63,0	78,8	124,5	110,2
Spongy mesophyll ..	135,0	247,5	193,8	355,5
Lower epidermis	22,5	22,5	22,5	24,8

These values are of considerable interest in view of recent investigations by LOHR (1919) as to the structure of the leaves of *Myosotis alpestris* SCHMIDT at different altitudes in the Alps. The increase in leaf thickness in higher altitudes, according to him, is due to the increase of the spongy mesophyll, while the depth of the palisades decreases. Our alpine material (the Finse type) behaves much in the same way when compared with the subalpine Torne Träsk material, but does not do so when compared with the subalpine Dovre material. As far as I am able to judge from my own cultivated material, collected at different altitudes in the Alps, the inequalities are, no doubt, due to hereditary differences between the Scandinavian and the Alp material, and to the fact that the alpine type of *M. alpestris* in the Alps represents only a high altitude modification of the subalpine type. Thus the inequalities, on the one hand, between our subalpine material and the Alp type and, on the other hand, between the subalpine types of Dovre and Torne Träsk are no doubt hereditary in nature. The further question whether or not these genotypical differences are the expression of different directions of the selection processes within the population in response to the climatical differences in the north and the south and in the Dovre and Torne Träsk districts or only chance isolations cannot be settled at present.

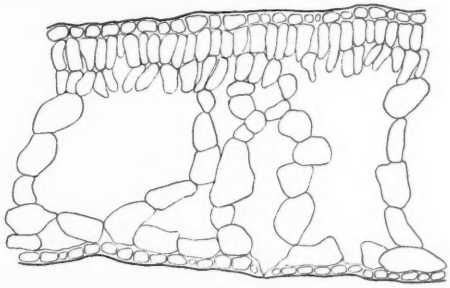

Fig. 20. Cross section of a radical leaf of the cult. alpine type (Finse) of *Myosotis silvatica*. Drawn with a Zeiss camera lucida. × 80.

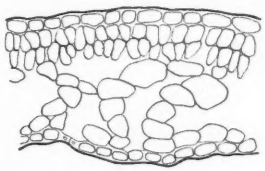

Fig. 21. Cross section of a radical leaf of the cult. southern type of *Myosotis silvatica*. Drawn with a Zeiss camera lucida. × 80.

The material from Dovre and Torne Träsk as well as other Scandinavian series not mentioned above have, however, so many characteristics in common that it seems most reasonable at present to group them into one type, the *subalpine ecotype* of the species. This is distributed mainly in the subalpine region, but is also found higher up in more protected situations. The Finse type represents

a far more extreme type and is here classed as the *alpine ecotype*. It grows in the alpine region and has so far only been found at Finse, although it may also occur in other alpine regions, at least in Norway.

9. ECOTYPES OF GEUM RIVALE L.

Numerous series of this species have been brought in culture, both from the Scandinavian peninsula and from Germany and Austria. Only the Scandinavian material will be considered here. This comprises series from Scania, Öland and Västergötland (collected in 1920 and 1921), from Torne Träsk in Lappland (coll. 1923), from different places along the west coast of Norway (Bodö and Brönnöy, coll. in 1922 and 1923), as well as from Finse in the Hardanger district (coll. 1922). Awaiting the results of crosses between the different types clone series have been raised from individuals transplanted from Torne Träsk, Bodö and Finse.

When compared in culture the material is found to group itself into three types. The Finse material, which comes from the alpine region about 1325 m. sup. m., represents by far the most extreme type. It is lower in stature, with smaller radical leaves than the lowland type of southern Sweden, but is much more rigid than this latter. Table 7 gives two series, the lowland type (from Åkarp) and the Finse type. The values are average values obtained from measurements of five stems and five leaves (the terminal segment of the radical leaves) of each individual. The Finse type flowers also somewhat earlier than the lowland type. The clone series of Finse individuals repeat exactly the same characteristics as shown by the older transplants. Thus the results of the cultivation must be said to favour strongly the assumption that the differences now seen in the cultures are due to genotypical differences. The way in which the original transplants responded to the less extreme, cultural conditions also supports this conclusion. In its natural habitat, the alpine region, the plant is much dwarfed and is usually one stemmed. The average height of the Finse series, when collected in 1922, was 225 mm. Already in the following year the average height of the individuals was about the same as in 1924, or 467 mm. The greatest increase in height takes place the year following the transplantation, and the subsequent increase has been but slight, while the increase in bulkiness progresses every year. The plants in question behave much in the same way as those of a certain dwarf population of

Succisa described before (TURESSON 1922). Fig. 22 gives a good picture of the Finse type (to the left) and of the lowland type from Åkarp (to the right).

The material from Lappland comes from much the same loca-

TABLE 7. *Geum rivale, from Scania (Åkarp No. 624) and Finse (No. 334).*

No. 624 in culture since 1921, No. 334 since 1922. Notes taken 1924.

Field number	Length of stems in mm.	Width of radical leaves in mm.	Field number	Length of stems in mm.	Width of radical leaves in mm.
624, 1	609	105	334, 1	561	70
2	606	99,3	2	517	82,6
3	631	108,3	3	518	62,3
4	648	118	4	462	62,5
5	643	106,8	5	499	66
6	724	160,7	6	462	66,6
7	554	122,3	7	511	67,6
8	687	120	8	468	87,3
9	580	124,3	9	497	71,6
10	646	93,6	10	490	70,7
11	685	119	11	414	72,7
12	644	102,3	12	513	82,3
13	568	98,3	13	458	74,3
14	562	99,6	14	486	66,7
15	721	110	15	561	65
16	642	125,3	16	449	65
			17	483	62,7
			18	488	75
			19	407	61,5
			20	438	77
			21	402	61,3
			22	483	62,7
			23	521	71,3
			24	550	67,7
Average in mm.	634,4	113,29	Average in mm.	484,9	70,1

lities as that of the subalpine *Myosotis* material, while the Norwegian coast material has been collected in rich meadows at sea level. The series resemble each other very much but differ markedly from the above mentioned. The plants are about as tall as the lowland type but have larger flowers and leaves, and the leaf regeneration at the base of

stem is powerful. The calyx lobes are longer and narrower than in the other types. The clone series raised from Torne Träsk and Bodö individuals show the same characteristics. That these characters are of a hereditary nature and not modifications called forth in direct response to habitat conditions seems therefore clear.

As to the anatomical structure of the leaves the differences between the cultivated types are not great. The Finse type has somewhat thicker radical leaves than the other types, and the palisade

Fig. 22. ***Geum rivale.*** **Cult. individuals of the alpine type (on the left) and of the lowland type (on the right).**

layers, usually two in number, have been increased in this type with a third layer.

The grouping of the entire Scandinavian species-population of *Geum rivale* into ecotypes cannot be accomplished at present, especially as the lowland type of the soufhern part of the peninsula has not yet been adequately compared with types from farther south. The boreal material, however, falls into two natural groups: the *subalpine ecotype* and the *alpine ecotype*. The former has probably an extensive distribution in the subalpine regions of North Scandi-

navia and occurs likewise at sea level, at least along the upper part of the west coast of Norway. The former has so far only been located at Finse, where extreme alpine conditions prevail.

The subalpine ecotype as delimited above has aroused the interest of systematists. It has been described (from Bodö!) as f. *subalpinum* by NEUMAN (1905). As to the nature of *G. rivale humile* SCHUR., distributed in the Alps and in the Carpathians at high altitudes, nothing can be said at present, as no cultural experiments have been undertaken with this form.

10. ECOTYPES OF LEONTODON AUTUMNALIS L.

The cultivated material of this species has been much increased since the publication of the last report in 1922. On account of the perplexing variation characteristic of this species the grouping of the Scandinavian species-population into ecotypes is a very laborious task. There are two types, in addition to the coast type described previously (TURESSON 1922), which are rather homogeneous in habitus however. One of these, the *Alfvar ecotype,* grows abundantly on Öland and, presumably, on Gotland. Cultivated material of this type, collected in 1922 and 1923 in different localities on Öland, has extremely narrow leaf lobes, much depressed foliage and stems, and involucres slightly pubescent, sometimes pilose. Most of the individuals in their natural habitat match the description given to var. *coronopifolius* LGE (see OSTENFELD 1913), as has also been pointed out by workers on the Alfvar flora (ERIKSON 1901, WITTE 1906 a). The anatomical structure of the leaves of this type differs from other types in being isolateral (cf. fig. 23). The results of the cultivation of transplants as well as of clone series, which have also been raised, leave little doubt as to the genotypical nature of these characteristics.

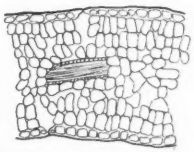

Fig. 23. Cross section of a leaf of the cult. Alfvar type of *Leontodon autumnalis.* Drawn with a Zeiss camera lucida. × 80.

The cultivated material comprises also series from the central Scandinavian mountain district (Jämtland and Härjedalen), Lappland, Lofoten islands and from several places along the coast of Norway, as well as from Finse. The discussion of most of this material will be postponed for the present. However, the series from extreme alpine localities, viz. the series from Åreskutan 1200 m. sup. m. (coll. 1922) and from Finse 1250 m. sup. m. (coll. 1922), deserve to be

mentioned already now. In their natural habitat the plants of these series are low dwarfs, at most 10 cm. high, and match the f. *taraxaci* (L.). Already after one year of cultivation the plants become taller, but the height now attained does not become greater in the following year. The average height of the Finse series measured in the cultures in 1924 was 287,2 mm., the average height of the cultivated series from Åreskutan measured the same year was 265,4 mm. Inland series from the southern part of the country cultivated side by side

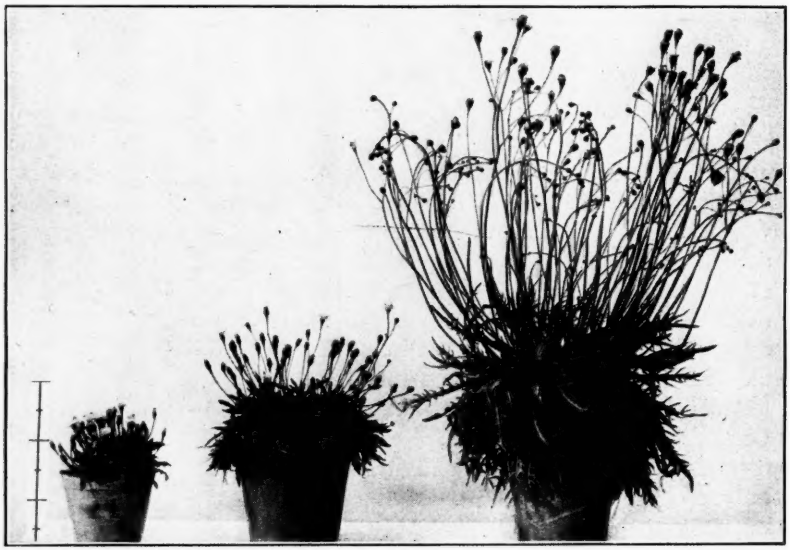

Fig. 24. *Leontodon autumnalis.* Cult. individuals of the alpine type (the two on the left) and of the Ottenby series (on the right).

measured the same year between 420—530 mm. in height. The lower stature of the alpine series is repeated by the clone series, which were raised in 1923 from individuals of both series. It is thus seen that the dwarf growth of the alpine individuals is only partly due to modificatory dwarfing in response to extreme habitat conditions, while on the other hand the individuals composing the population in extreme alpine situations are no doubt genotypically lower in stature than individuals inhabiting less extreme localities. The alpine types investigated have all strongly pilose involucres and flower earlier than lowland series.

In places, where different types come together, bastards representing different combinations are met with. Along the coast of Norway alpine forms mix with coast forms and a bewildering series of different biotypes is found. In Äre and other places in Jämtland the population contains alpine and more southern forms together with their bastards. Most of these bastard individuals match the f. *asperior* WG.

Isolated bits presumably of the mountain population are sometimes found in the southern parts of the country. Such an isolation has been located near Ottenby on Öland (Schäferiängen), where individuals seemingly identical with f. *asperior* are found abundantly on the shore. The relict nature of this as well as of other similar populations on Öland will be dealt with in a subsequent paper. Fig. 24 shows the extreme alpine type (the two individuals to the left) and the *asperior* type at Ottenby (to the right).

The cultural experiments have clearly demonstrated the fact that only relatively few of the mass of different biotypes contained in a mixed population are able to populate such extreme habitats as the Alfvar of Öland and *regio alpina*. We designate these two types for the present as the *Alfvar ecotype* and the *alpine ecotype*.

A few words should be said of the systematical treatment of the species. NEUMAN (1882—83) in our country discusses various forms, some of which have been dealt with in a previous paper (TURESSON 1922). Subsequent attempts made by systematists to bring order into the mass of existing biotypes cannot be said to have added much to the attainment of a better survey of the variations. Indeed, a systematization of the species-population along traditional, systematical lines has every prospect of being unsuccessful. The existing confusion is by no means done away with by the raising of different biotypes to the rank of subspecies, as is done by PERSSON (1913). To those, however, for whom the increase and the naming of »new» biotypes is a particular pleasure, as well as to other intending bidders, I am willing to offer a couple of hundreds hitherto undescribed ones in a living and exquisite condition.

11. ECOTYPES OF RANUNCULUS ACER L.

Sets of this species have been collected from a great many places in the Scandinavian peninsula as well as in the Alps during the last few years. Only some of the series, cultivated since 1922 and earlier,

will be considered here. The collections of alpine dwarfs brought home from Finse, Åreskutan and Lappland (Nuolja) are of particular interest, and the discussion will therefore centre upon these series. The Finse series (coll. 1922, 1400 m. sup. m.) comes from the *Dryas*-rich lichen heath, which SAMUELSSON (1917) has described in his paper on the vegetation of Finse. The Åreskutan series (coll. 1922) comes from meadows at about 1000 m. sup. m., and the Nuolja

Fig. 25. *Ranunculus acer.* Dried and mounted individuals from the alpine region at Finse. The plant on the upper right hand corner 85 mm.

series (coll. 1923) comes from a similar habitat at about 900 m. sup. m. The Nuolja plants were the lowest in stature when collected and did not reach 100 mm. in height. The plants from Åreskutan measured 160 mm. on the average, and those from Finse averaged 120 mm. (see fig. 25). The behaviour of these series when cultivated is very different. Already the first year after being transplanted the differences may be seen. The Åreskutan series now attains the same height as that characteristic of the plant in the lower regions and in the southern part of the country, while the Finse series does not reach this height. Table 8 gives the height

TABLE 8. *Ranunculus acer from Stehag (No. 623), Finse (No. 265), Frösön (No. 280) and Åreskutan (No. 380).*
Plants cultivated since 1922. Notes taken 1924.

Field number	Length of longest stem in mm. (when stretched)	Field number	Length of longest stem in mm. (when stretched)	Field number	Length of longest stem in mm. (when stretched)	Field number	Length of longest stem in mm. (when stretched)
623, 1	558	265, 1	510	280, 1	695	380, 1	644
2	747	2	609	2	622	2	668
3	554	3	567	3	—	3	—
4	641	4	493	4	643	4	581
5	638	5	—	5	604	5	678
6	768	6	535	6	584	6	567
7	759	7	406	7	668	7	572
8	563	8	553	8	528	8	585
9	782	9	498	9	572	9	—
10	594	10	614	10	677	10	653
11	504	11	588	11	659	11	748
12	513	12	365	12	668	12	578
13	703	13	727	13	652	13	706
14	659	14	423	14	499	14	512
15	568	15	—	15	577	15	702
16	588	16	449	16	689	16	698
17	609	17	457	17	505	17	546
18	492	18	412	18	646	18	—
19	714	19	594	19	776	19	693
20	611	20	642	20	626	20	—
21	636	21	334	21	672	21	—
22	643	22	473	22	691		
		23	538	23	812		
		24	637	24	782		
		25	644	25	696		
		26	368	26	684		
		27	406				
Average in mm.	629,27		513,68		649,08		633,18

differences as seen in 1924 in the series transplanted from Stehag (in Scania), Finse, Jämtland (Frösön) and Åreskutan. The results from the cultures, comprising the last two series as well as those from others, not listed here, go to show that the alpine dwarf of the species occurring at high altitudes in Åreskutan (and presumably in

other mountains in the central Scandinavian mountain district) is merely a dwarf modification. Compared with these series the Finse plants are on the average lower. The same is true when the series from Finse is compared with Norwegian series transplanted from lower regions. Such series, transplanted in 1921 and 1922 from Trondhjem, Molde, Voss and Bergen, are on the average 100 mm. taller in the cultures than the Finse series. It is therefore reasonably safe to assume that the alpine dwarf of Finse, although to a great extent a product of the direct effects of the extreme habitat, differs

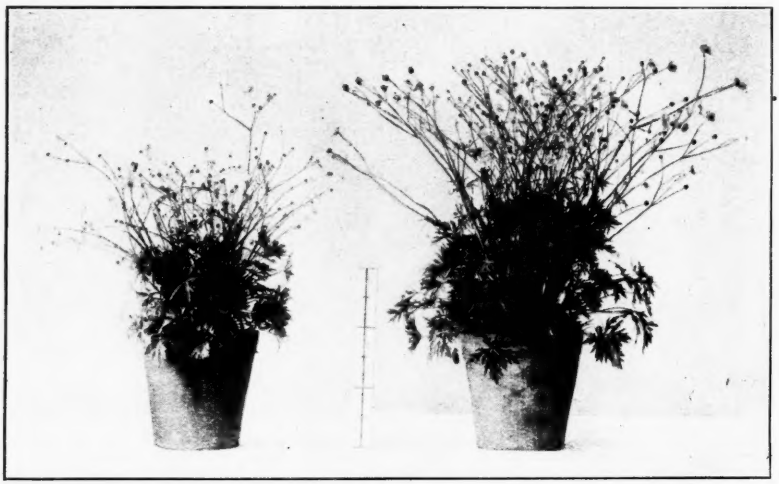

Fig. 26. *Ranunculus acer.* Cult. individuals of the alpine type (Finse).

genotypically as to the height factors from the plant of lower regions.

It seems also clear that the Nuolja dwarfs, although young in the cultures, also differ genotypically from the subalpine type of the species so common around Nuolja (Abisko, Björkliden). Cultures of such series attain on an average the same height as those from Jämtland, while the Nuolja series is very much lower in stature. The details of the Lappland series will be postponed till another occasion.

There are additional differences, however, between the cultivated Finse plants and the cultivated plants of the lower region of Norway and those from Jämtland. The flowers are considerably larger, the

time of flowering falls earlier, and the leaf thickness, which in the other series is about 300 μ, measures in the Finse plants about 400 μ.

The growth form of the Finse plants is also somewhat different from the usual. The stems are more spreading, and the leaves show a tendency to collect at the base (cf. figs. 26 and 27).

The marked differences between the alpine type of Finse and the alpine type of Nuolja is a further interesting fact. Apart from

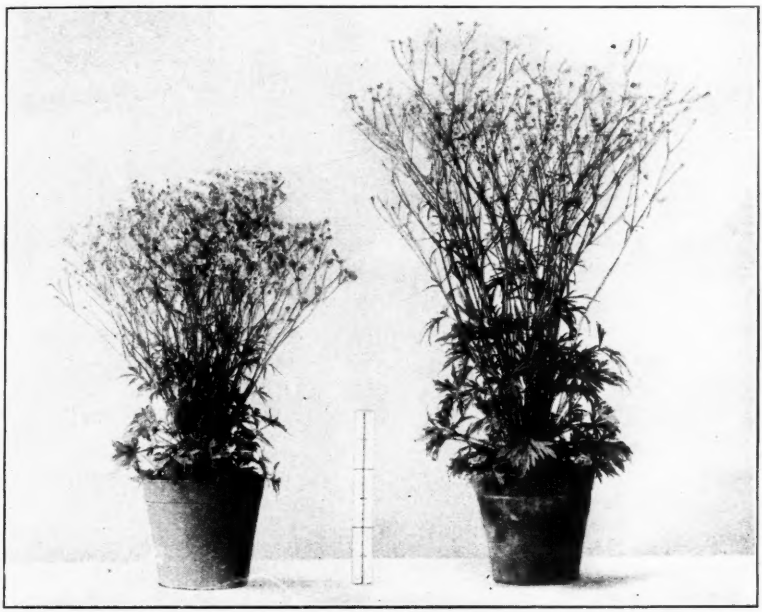

Fig. 27. *Ranunculus acer.* Cult. individuals of the southern type (Stehag).

differences in leaf shape the Finse plants have a more or less dense covering of yellowish-brown hairs on the stems and petioles, while the Nuolja plants lack such hairiness. As to the hairiness and other characteristics the Finse plants show great similarities to the type of the species growing along the Norwegian coast (as well as on Iceland and on the Faroe Islands). The Finse type, no doubt, has become differentiated from this Atlantic population, while the Nuolja type has probably quite another origin. That both are of the nature of *alpine ecotypes* and as such are limited to *regio alpina* seems unquestionable.

Our Finse and Nuolja plants have both been called f. *pumilus*. The *pumilus* form of WAHLENBERG, however, covers only the Nuolja plant, not the Finse plant. Other *pumilus* forms in systematic handbooks embrace probably both wholly modificatory dwarfs matching our dwarfs from Åreskutan and plants combining a genotypically lower stature with habitat dwarfing (matching our dwarfs from Finse). Genotypically low growing alpine types of *Ranunculus acer* seem to be entirely wanting in the Alps and the Carpathians. My own cultivated dwarf material from the Alps is assuredly modifications only, which, when growing in their natural habitat, match the var. *subalpinus* STROBL. (syn. *parvulus* CLAIRVILLE). It is interesting to note that HEGI (1906 —), among others, also stamps this form as an »alpine Kümmerform».

12. ECOTYPES OF MELANDRIUM RUBRUM (WEIG.) GARCKE.

Efforts have been made to collect this species from as many points as possible within its European area of distribution. Although several hundred transplants of the species are under culture only a few of these will be considered on this occasion. Two different types of the species, a thin leafed inland type from the beech woods of Scania, and a thick leafed coast type from the cliffs at Kullen in N. W. Scania, have been described in a previous paper (TURESSON 1922). Attention was also drawn on that occasion to alpine varieties even more fleshy than the coast type. More extended cultures of these types have strengthened the view as to the existence of hereditary widely different ecotypes within the population. The thin leafed inland type seems limited to the extreme southern part of the country, where it grows abundantly in the beech woods. In the cultures this type flowers about 14 days later than the other types. The thick leafed coast type has been located at different points on the west coast and on the east coast (Kullen, Hallands Väderö, Lysekil on the west coast; Kalmar, Västervik, Stockholm archipelago on the east coast). While the leaf thickness of the southern inland type measures 300—450 μ (in this and in other types mentioned below the measurements refer to well-developed rosette leaves collected in the cultures in autumn) the coast type measures 425—615 μ. The number of palisade layers never exceeds 2 in the former type, while it is often 3, sometimes 4, in the latter and in the other types to be mentioned later.

It is a difficult task to delimit the boreal type of this species from the coast type of the southern part just mentioned. The attempt in this direction made by SIMMONS (1907), which is based mainly on differences in hairiness, cannot be said to be conclusive when it is seen that individuals might be found in Lappland which, as regards type of hairiness, match the type said to be characteristic of the southern part of the country. However, the series transplanted from

Fig. 28. *Melandrium rubrum.* Dried and mounted individuals from the alpine region at Finse. The plant on the lower right hand corner 135 mm.

the northern parts of the country (Luleå, Abisko, Örnsköldsvik, Jämtland) have been found to have somewhat thicker leaves than the southern coast type (from 500 μ to 680 μ), the basal leaf rosette attains greater dimensions in the course of the vegetation period and the flowering period falls somewhat earlier. Additional differences will be treated more fully on another occasion. Further, these plants seem to correspond in details to the subalpine type found in the Alps and in the Carpathians and now cultivated on a large scale in the experimental fields.

There exists, however, still another type of the species, which seems limited to *regio alpina*. This type is so far represented in the cultures only from Finse (in culture since 1922; coll. at 1450 m. sup. m. in lichen heath) although it doubtless occurs in other places in Norway and Sweden. It is usually much dwarfed in its natural habitat; the average height was found to be 135 mm. Individuals are sometimes found which measures up to 230 mm., and pygmies not exceeding 60 mm. are also found. Fig. 28 shows the two extremes in the collection brought home in 1922, as well as one individual (lower right hand corner) of average size. When transplanted an average height of about 340 mm. is attained already in the following

Fig. 29. *Melandrium rubrum*. Cult. individuals of the alpine type (Finse).

year, and this average height has also been maintained during 1924. The average height of the rest of the other types, cultivated side by side, varies between 400—550 mm.

In considering the height-differences of the various series it should be noted that as a rule the males are lower in stature than the females. The average values of series, which comprise more females than males, therefore become greater than in series where males are rare. The Finse series includes only two males, while the rest (10) are females. The proportions between males and females seem to be fairly equal in the rest of the material (see, however, CORRENS 1921). Fig. 29 (cf. also BAUR 1914, fig. 122) shows representative individuals from the cultivated Finse series (the two males to the left), and fig. 30 shows a male (to the left) and a female

plant (to the right) from a cultivated coast series (transplanted from Kalmar).

The results of the cultural experiments clearly show that the dwarf habitus is not merely a habitat modification; there must be present also genotypical factor differences between this and the other series. There are, however, additional differences. The leaf thickness is much greater in the cultivated Finse series, it sometimes

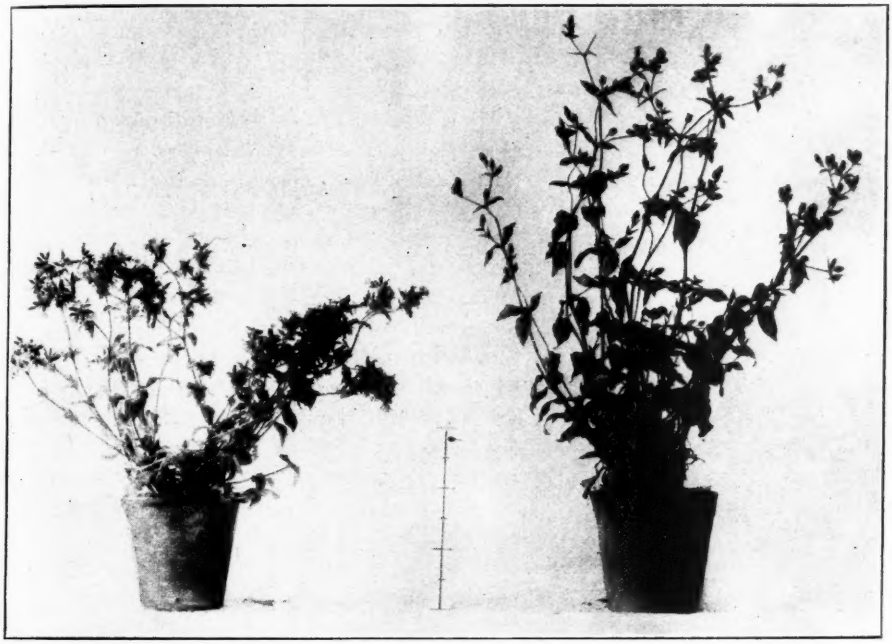

Fig. 30. *Melandrium rubrum.* Cult. individuals of the southern coast type (Kalmar).

attains a value of 765 μ. The rosette formation is also still more marked here than in the other series. For the rest, there are considerable variations. Individuals with entirely glabrous leaves and stems are found, and the colour of the flower varies from pink to dark red.

That the leaf thickness found in this type is of hereditary nature and not a modificatory character is seen from the fact that the leaves of the Finse series have become throughout thicker during cultivation. Fig. 31 shows the general appearance and thickness of

the leaf of the Finse type while growing in its natural habitat, while fig. 32 shows the appearance and thickness of the leaf of the same individual in culture in 1924.

Although much remains to be done before a clear understanding of the different types is reached the differences in hereditary composition, which the species-population exhibits at different points within its geographical area of distribution, are too striking to be left unconsidered. The thin leafed inland population in the south of the country probably represents the northern extension of the lowland population of Middle Europe (as cultivated series from Middle Europe go to prove). The changes in the species-population in northern Scandinavia, where thick leafed, early flowering individuals dominate, are doubtlessly brought about by the sorting effect of the climate upon the species-population. The correspondence between this boreal population and the subalpine population of the Alps tends to strengthen this view. The coast type of the southern and middle parts of Sweden shows resemblances in habitus to the boreal type. It may also be that the boreal type runs down along the coast strips in the same manner as some alpine plant species are known to do (cf. the distribution maps of *Alchemilla alpina, Carex aquatilis* and *Silene rupestris* in HÅRD AV SEGERSTAD 1924). If this be true, however, the differences between the coast type and the boreal type must be explained. The differences may be due to hybridisation with the southern inland type, or they may be due to changes which the boreal population undergoes in response to the climate of the southern and middle parts of the country. A thourough investigation of the nature of the inland population of Middle Sweden will probably bring light on this question. That the extreme alpine type, as instanced by the Finse series, is also brought about by the differentiating and sorting

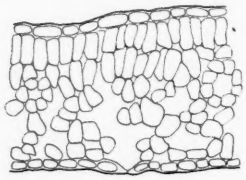

Fig. 31. Cross section of a radical leaf of the alpine type of *Melandrium rubrum* growing in its natural habitat. Drawn with a Zeiss camera lucida. × 60.

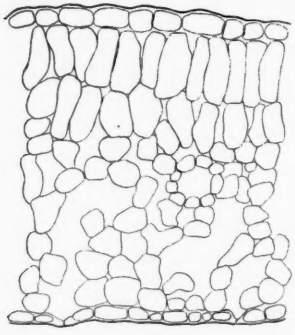

Fig. 32. Cross section of a radical leaf of the same individual as in fig. 31 now under cultivation. Drawn with a Zeiss camera lucida. × 60.

effect of the extreme habitat factors upon the populations appears more than likely.

The material hitherto dealt with may roughly be grouped into the following ecotypes:

a. *The southern inland ecotype.*

b. *The coast ecotype* of Southern and Middle Sweden.

c. *The subalpine ecotype* of Northern Scandinavia and of the subalpine regions of the Alps and of the Carpathians.

d. *The alpine ecotype* of Northern Scandinavia. Entirely wanting in the Alp range.

As regards the systematic and nomenclative side of the question a few words may be added. Part of the complex, which we have called the subalpine ecotype, has been called subsp. *lapponicum* by SIMMONS (1907). The most extreme dwarfs of our alpine ecotype (those up to 60 mm.), as seen in the natural habitat, have been called var. *subacaulis* by NORMAN (1893). Glabrous individuals, presumably of this ecotype, have been called var. *alpestre.* (*Melandrium Preslii* SEIDL. is a glabrous variety, presumably of the southern inland ecotype; cf. DE VRIES 1903). Individuals, probably of the thick leafed coast ecotype, have been called var. *crassifolium* by FRIES, who has distributed dried specimens of the plant with the following label record: »Cat. Hort. Ups. s. *Melandrium maritimum* FR. mscr. In Norvegia occid. (Christiansand) semina legit EKMAN, e quibus educatum per decennium in H. Ups. constans et jam in Hort. frequens».

13. ECOTYPES OF RUMEX ACETOSA L.

Much material of *Rumex acetosa* and its allies (*R. arifolius* and *R. thyrsiflorus)* is now in culture in the experimental fields. The relation of *R. acetosa* to the allies just mentioned will not be treated on this occasion; neither will the hereditary differences seen in series of the latter forms, for instance in *R. arifolius,* where the Scandinavian material shows marked differences from the material collected in the Alps, be dealt with here. The following discussion will serve to emphasise the fact that within the *acetosa* population proper definite types have become differentiated in response to definite climatic conditions.

The differences are best seen in regard to height. The series from the southern part of Middle Europe are on the whole taller than those collected in the southern part of Sweden. The height of the female individuals in series from Freiburg i. Br. (cultivated since

TABLE 9. *Rumex acetosa from Bökeberg (No. 707) and Finse (No. 261).*
Plants cultivated since 1922. Notes taken 1924.

Field number	♀ Length of longest stem in mm.	♂ Length of longest stem in mm.	Length of basal leaves	Width of basal leaves	Field number	♀ Length of longest stem in mm.	♂ Length of longest stem in mm.	Length of basal leaves	Width of basal leaves
707, 1	1020	—	72	33	261, 1	570	—	65	27
2	1250	—	59	29	2	250	—	52	29
3	800	—	51	27	3	420	—	64	28
4	780	—	56	24	4	—	350	65	29
5	1120	—	82	37	5	440	—	62	21
6	880	—	62	31	6	450	—	69	37
7	—	510	60	29	7	450	—	44	26
8	1080	—	72	32	8	490	—	74	36
9	900	—	69	31	9	—	—	62	30
10	1320	—	72	34	10	650	—	56	31
11	1000	—	54	30	11	420	—	—	—
12	—	600	52	28	12	400	—	62	30
13	—	480	51	25	13	—	320	54	26
14	1020	—	72	36	14	600	—	55	25
15	—	650	64	36	15	—	400	60	31
16	—	600	59	28	16	360	—	58	20
17	—	540	68	30	17	350	—	85	40
18	980	—	57	30	18	430	—	72	36
19	650	—	64	33	19	180	—	—	—
20	—	680	70	32	20	470	—	80	42
21	1170	—	58	30	21	820	—	75	30
22	—	450	59	28	22	—	—	—	—
23	840	—	70	32	23	450	—	60	28
24	1000	—	62	32	24	780	—	76	40
25	—	600	62	34	—	—	—	—	—
26	—	640	62	31	—	—	—	—	—
27	—	530	74	35	—	—	—	—	—
28	1160	—	60	28	—	—	—	—	—
29	—	600	72	36	—	—	—	—	—
30	1180	—	68	30	—	—	—	—	—
Average in mm.	1008,3	573,3	63,76	31,03		472,6	356,6	64,28	30,57

1922) and from Wien (cultivated since 1921) averages 1060 mm., while the females of series from South Sweden (Bökeberg in Scania, cult. since 1922; Furulund in Scania, cult. since 1922; various series from Blekinge, etc.) average 1000 mm., in some series somewhat less.

The former plants are also more thick stemmed and more robust than ours. The extreme in the other direction is shown by the alpine type of the species, as yet in culture only from one locality, viz. from Finse (coll. 1922), where it grows abundantly in the alpine meadows at about 1400 m. sup. m.[1]. It is considerably dwarfed here; in 1922 it averaged 140 mm. in height (see fig. 33).

When cultivated the individuals of this type show an increase

Fig. 33. *Rumex acetosa.* Dried and mounted individuals from the alpine region at Finse. The plant on the right 125 mm.

in height already in the following year. The height now attained does not alter in the next year but remains fairly constant. Table 9 gives the height-differences seen in 1924 in a series from Scania (Bökeberg) and in the Finse series. While the females of the former series average 1000 mm. the females of the Finse series do not attain half of this height. The length and width of the basal leaves of the two series, derived by measuring five leaves of each individual, da

[1] SAMUELSSON (1917) records also *R. arifolius* from Finse. I did not succeed in finding this form during my stay in Finse in 1922.

not show any marked differences. The Finse type differs also in other respects from the more southern typer. It flowers earlier, the leaves are thicker and shining green in colour, and the flowering stems are less erect than in the southern type. It is, moreover, a typical cushion plant, which in the height of summer develops a large, basal leaf cushion (cf. figs. 34 and 35), while the southern type does not develop a ground rosette of small dimensions until the beginning of autumn.

The type growing in the central Scandinavian mountain district (transplanted from different localities in Jämtland) shows resemblances to the type growing along the northern portion of the west coast of Norway. It is intermediate in height between the alpine and the

Fig. 34. *Rumex acetosa.* Cult. individuals (♂ and ♀) of the alpine type (Finse).

more southern type and represents in all likelihood a subalpine type of the species.

The characteristics of the different types of *Rumex acetosa* have been further worked out by Mr. D. PETERSON, who, in a paper to be published later on, records marked differences in the number of stomata in the different types, as well as other peculiarities ecologically related to habitat and climate.

In most of the cultivated material there is a great disproportion between the number of males and females. In some series the number of males and females has been counted, and the following relation found:

Locality	Number of individuals	Number of females	Number of males
Bökeberg, Scania	30	18	12
Stehag, »	28	20	8
Furulund, »	11	9	2
Marielund, Blekinge ..	24	22	2

Locality	Number of individuals	Number of females	Number of males
Åreskutan, Jämtl.	23	19	4
Svolvær, Norway....	11	10	1
Bergen, »	9	8	1
Finse, »	22	19	3
Wien	19	17	2
	177	142	35 (about 20 % ♂)

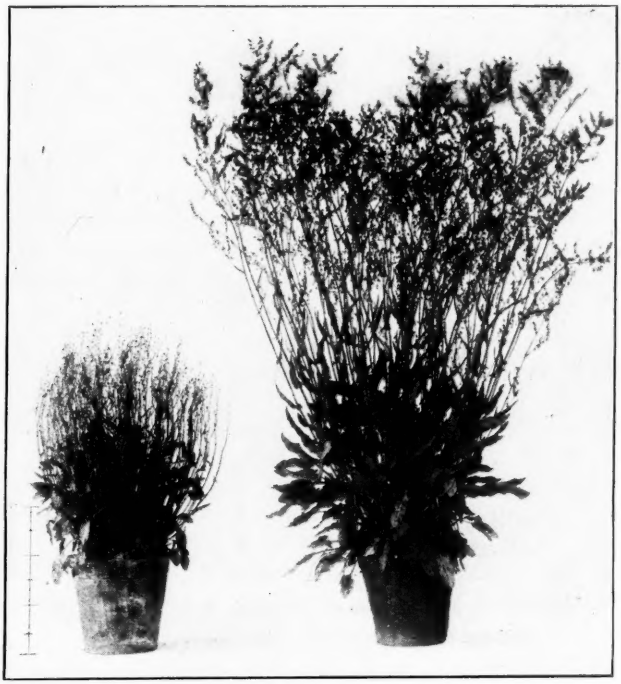

Fig. 35. *Rumex acetosa*. Cult. individuals (♂ and ♀) of the lowland type.

This disproportion between the males and females in *Rumex acetosa* has been discussed by several workers (HOFFMANN 1885; in *R. thyrsiflorus* by RAUNKIÆR (1918 a). CORRENS (1922), however, adduced proofs that the mechanical sex proportion 1 : 1 is displaced on account of the fact that the female determining pollen tubes grow faster and reach the egg cells more rapidly than the male determining ones, and that the death rate in the male embryos is higher than in

the female. The full grown males were also found to have a higher death rate than the female plants. The marked difference in height (see table 9) between females and males becomes of interest in this connection. This difference in height has been noted and discussed by SPRECHER (1913) and CORRENS (1922). I am under the impression that the disproportion between males and females is greatest in habitats with rich and dense field strata. The first two series listed above (Bökeberg and Stehag) come from bare ground on lake shores, while the rest of the series comes from habitats with dense field strata, where competition is presumably severe. The lower stature of the males might well be thought to place these plants at a special disadvantage thus secondarily increasing the disproportion already existing.

As to the grouping of the species-population into ecotypes the Finse type, on account of its striking characteristics (low stature, cushion growth, early flowering, etc.) and its distribution in *regio alpina,* must be considered as the *alpine ecotype* of the population. The type of the central Scandinavian mountain district and of the upper Norwegian coast probably represents a *subalpine ecotype,* which, however, needs further study and comparison with the southern ecotypes of the species before being accepted.

It should be added that alpine dwarfs of *Rumex acetosa* have not been recorded by systematists. *R. acetosa alpinus* in ASCHERSON and GRAEBNER (1908—1913) is typical *R. arifolius* ALL. (syn. *R. acetosa β alpina* L., Fl. suec. ed. II. p. 119; HARTM. Skand. fl. ed. XI. — *R. acetosa β alpestris* HARTM. l. c. ed. II. — *R. montanus* DESF.). Alpine dwarfs of *Rumex acetosa* are entirely wanting in the Alps and in the Carpathians. They are substituted in the Alps by *R. arifolius β nivalis* DUTSCHM. (syn. *R. nivalis* HEGETSCHW.).

14. ECOTYPES OF CAMPANULA ROTUNDIFOLIA L.

Sets of this variable species have been collected from a great many places on the Scandinavian peninsula, as well as from Germany, Austria, Hungary, and the Alp range. Most of the material is too young to be considered here, and therefore only a few of the older series will be discussed in the following pages to the extent necessary to show the differentiation of ecotypes in the species. The series to be discussed are tabulated in tables 11—19, and they have been transplanted from Vitemölla (1920) and Åhus (1922) in Scania, from

Ulriksdal, near Stockholm (1921), from Åre in Jämtland (1921), from Bergen (1922) and Trondhjem (1922) in Norway. In addition a series of plants raised from seeds from Abisko in Lappland (1921) will be discussed, and also two young series from Germany (Freiburg i. Br., and Feldberg in Schwarzwald at about 1300 m. sup. m.), both transplanted in 1923. In order to facilitate the survey of the different series the following table (table 10) gives the average values obtained for the characteristics investigated in each series.

TABLE 10.

Nos.	Transplanted from	Length of stems in mm.	Width of middle stem leaves in mm.	Number of flowers on stems	Length of corolla in mm.	Width of corolla in the middle	Width of corolla at mouth	Length of corolla lobes in mm.	Length of calyx lobes in mm.	Power of regeneration of basal rosette leaves
99	Vitemölla	547,75	2,18	23,25	18,63	16,50	22,45	7,33	6,33	none—weak
206	Åhus	650,54	2,16	27,49	19,93	16,45	22,82	7,65	7,29	»
270	Ulriksdal	334,30	1,86	20,33	17,13	14,99	20,2	7,02	5,63	»
298	Åre	308,43	2,97	11,5	22,12	21,0	25,91	9,54	5,88	mostly strong
349	Bergen	378,67	2,73	9,19	20,56	20,53	25,67	8,41	6,36	weak—strong
240	Trondhjem ...	336	2,03	15,97	21,0	18,34	25,06	8,39	5,80	»
19—25	Abisko (seeds)	250,10	1,99	13,97	24,47	20,48	27,68	9,32	7,90	strong
770	Freiburg	278,56	2,12	19,86	20,44	18,89	24,54	8,5	6,56	none—weak
796	Feldberg	224,66	4,29	6,88	23,45	21,82	25,32	8,76	7,89	strong

The values obtained for each individual in tables 11—19 are average values based on measurements of five stems, five leaves and five flowers of each plant. The power of leaf-regeneration has been graded none—weak—strong, and the observation of this characteristic has been made during the flowering period. As to the habitus of the plants in their natural habitats it should be said that the Åre plants were lower in stature when collected; they increased in height under culture and already in the following year (1922) they attained the height now kept, with slight variations in response to the varying weather conditions in the different years. They were further single flowered, a characteristic which already disappeared after one year's cultivation. The Åre plants showed great similarities to plants transplanted from Abisko in Lappland in 1923. With regard to the Feldberg series (No. 796; table 19) it should be said that these plants, at least while in their natural habitat, match the subsp. *Scheuchzeri* VILL.

Considering first the height of the plants in the different series it is at once seen that this varies considerably in the lowland series of the southern and middle parts of Sweden (Vitemölla, Åhus and Ulriksdal). The series from the central Scandinavian mountain district (Åre) and from Lappland (Abisko), however, are both, as might be expected, lower in stature than the lowland series (see figs. 36 and 37). The height differences seen in the German series, although young, point undoubtedly in the same direction: lower stature of the mountain plants. That this difference in height be-

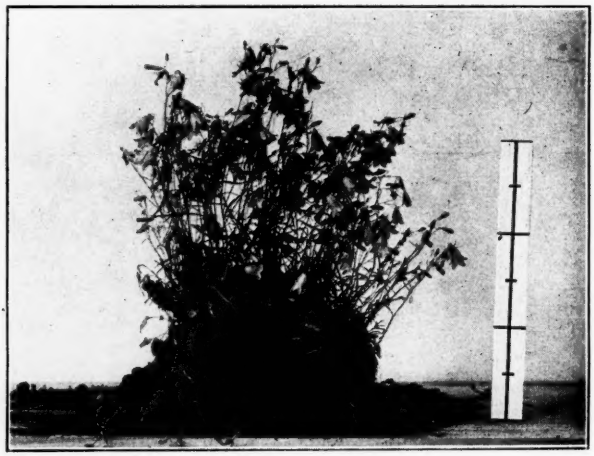

Fig. 36. *Campanula rotundifolia.* Cult. individual of the subalpine type (Åre).

tween the cultivated series is due to genotypical differences becomes more than plausible when the behaviour of the Åre plants (see above) and the dwarfishness of the Abisko plants, raised from seeds, are borne in mind.

The number of flowers on the stem has increased upon cultivation in the series, where single flowers were typical of the plants in their natural habitats, viz. in the Åre and Feldberg series. The differences as to this character now seen in the cultures between the lowland series and the mountain series might depend on genotypical differences.

One of the most striking characteristics of the series from alpine or boreal localities is the large flower. Not only is the length of the

corolla greater than in the lowland series, the width of the corolla, measured when flattened out, is also greater. The same is found to be true when the German lowland and mountain series are compared. When it is seen that this character is repeated year after year and when it is just as marked in the Abisko plants raised from seeds in 1921 as in the transplants from Abisko cultivated since 1923 little doubt remains as to the hereditary nature of this feature. The behaviour

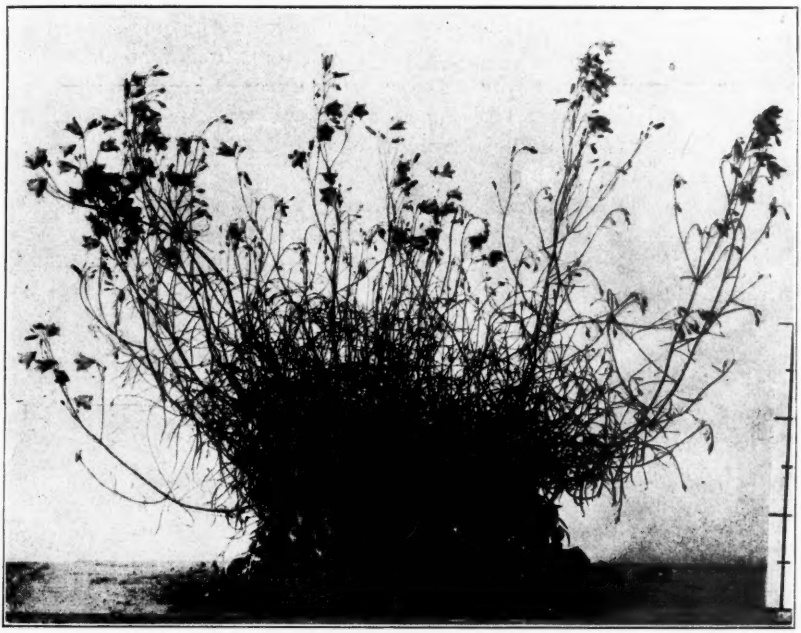

Fig. 37. *Campanula rotundifolia.* Cult. individual of the lowland type (Vitemölla).

of the lowland and the mountain types in places, where they come in contact with each other, furnishes another proof. Such mixed series have so far not been investigated in Scandinavia, but material collected in Schwarzwald and in the Alps is very elucidating. On Feldberg in Schwarzwald the intermediate area containing the mixed population lies between 800—1000 m. sup. m. Below 800 m. and above 1000 only the lowland resp. the mountain type is found. The intermediate area does not contain any uniform intermediate type, as one would expect were the two types merely modifications, but, on the

contrary, it is inhabited by a multitude of different combinations between the lowland and the mountain types together with fragments of both parents. Similar mixed *C. rotundifolia* populations are very common in the Alps in the lower subalpine region. Such mixed populations might also be found in Scandinavia, although the transitions naturally are sharper and more readily seen in the Alps, where the range in vertical line is great. Another feature, which at once stamps the type from Åre, Abisko and Feldberg as alpine, is the power of regeneration of the basal rosette leaves during the flowering period, which in these series is very marked, while none or weak in the lowland series. The material from the west coast of Norway (Bergen and Trondhjem) is mixed in this respect and in others, a peculiarity which thus the *C. rotundifolia* population has in common with other plant populations of this region as mentioned before.

The alpine and boreal types flower earlier than the lowland types and have in addition somewhat thicker leaves.

It is thus seen that the plant of the alpine and the boreal regions differs widely from that of the lowland. That the latter also varies (with the latitude) will be more particularly shown on another occasion. The Abisko type seems somewhat more extreme than the Åre type. It seems preferable at present, however, to group them together with the Feldberg type into one and the same ecotype, the *subalpine ecotype* of the species, so named because of the fact that the type seems to be distributed mainly in *regio subalpine* of the Alps and of the Scandinavian North. The similarities between the material from the Alps and from Scandinavia are great (stature, size of flowers, earliness, leaf regeneration), although differences also exist (in the width of the cauline leaves, as well as in the hairiness of the radical leaves of the Alp material). The different course of the differentiation process of the subalpine ecotype in the Alps and in Scandinavia will be further dealt with below.

There exists no doubt other ecotypes, alpine and lowland ecotypes, within the species, the treatment of which has to be postponed until the cultivated material, and the experience of the material already in culture, has increased.

As to the treatment of our subalpine ecotype by systematists it suffices to state that the habitat modification of the subalpine type matches the var. *Gieseckiana* (VEST) SIMM., while the habitat modification of the type, as found in the Alps, matches subsp. *Scheuchzeri* VILL.

TABLE 11. *Campanula rotundifolia No. 99, Vitemölla.*
Plants in culture since 1920. Notes taken 1924.

Field number	Length of longest stem in mm.	Width of middle stem leaves	Number of flowers on stems	Length of corolla	Width of corolla in the middle	Width of corolla at mouth	Length of corolla lobes	Length of calyx lobes	Power of regeneration of basal rosette leaves
1	604	2,32	28	18,0	16,4	23,6	8,2	6,6	none
2	468	1,48	11,8	17,8	15,9	21,3	6,5	6,4	weak
3	473	2,3	40,2	18,0	14,4	20,4	6,8	5,6	»
4	475	2,12	14,4	17,8	15,2	21,0	7,1	6,0	»
5	627	2,3	24,2	21,2	20,8	28,5	8,3	7,8	none
6	688	2,52	30,0	18,8	14,6	20,0	7,4	7,7	»
7	562	2,22	18,0	18,6	16,5	22,8	6,3	5,3	»
8	485	2,2	19,4	18,8	15,4	22,0	8,0	5,2	weak
Average in mm.	547,75	2,18	23,25	18,63	16,15	22,45	7,33	6,33	

TABLE 12. *Campanula rotundifolia No. 206, Åhus.*
Plants in culture since 1922. Notes taken 1924.

1	574	1,8	34,2	17,0	15,2	21,8	6,5	5,7	none
2	572	2,0	30,0	24,3	15,5	23,5	8,3	7,8	»
3	754	2,76	18,0	19,4	16,8	22,4	7,0	8,52	»
4	605	2,2	18,6	23,6	20,4	28,8	9,8	7,4	weak
5	634	2,1	28,4	18,2	16,4	22,2	7,1	7,4	none
6	758	1,7	35,2	20,0	15,8	23,2	7,4	8,6	»
7	648	1,8	29,2	20,4	16,8	23,2	8,2	8,8	weak
8	664	2,9	25,0	20,8	17,3	22,8	8,0	6,8	none
9	592	2,3	34,8	20,2	15,8	22,6	8,4	6,2	»
10	486	2,4	35,0	18,4	16,6	22,4	7,0	5,6	»
11	673	2,0	31,4	20,4	16,2	22,8	8,0	9,0	»
12	675	2,16	19,8	17,0	13,8	18,5	6,3	5,0	»
13	822	2,0	17,8	19,4	17,2	22,4	7,4	8,0	weak
Average in mm.	650,54	2,16	27,49	19,93	16,45	22,82	7,65	7,29	

TABLE 13. *Campanula rotundifolia No. 270, Ulriksdal.*
Plants in culture since 1921. Notes taken 1924.

1	343	1,8	28,4	15,2	14,0	19,4	5,9	4,9	none
2	356	2,2	18,8	18,3	14,8	20,5	6,5	6,0	»

Field number	Length of longest stem in mm.	Width of middle stem leaves	Number of flowers on stems	Length of corolla	Width of corolla in the middle	Width of corolla at mouth	Length of corolla lobes	Length of calyx lobes	Power of regeneration of basal rosette leaves
3	382	2,1	29,8	17,4	13,6	18,8	6,8	6,2	weak
4	320	—	—	—	—	—	—	—	none
5	359	2,0	12,2	16,8	13,4	18,0	6,6	6,2	weak
6	392	1,7	16,4	16,0	12,3	16,5	6,0	6,3	none
7	391	2,3	28,4	16,0	15,6	20,0	6,8	4,5	»
8	243	2,0	15,8	17,4	18,0	23,8	7,8	5,4	weak
9	328	1,5	12,8	14,6	12,4	16,6	6,0	3,8	none
10	390	1,9	21,8	17,4	16,4	21,8	7,4	4,0	weak
11	390	1,7	17,8	19,2	16,6	23,0	8,2	6,6	none
12	244	1,8	25,5	19,2	16,4	21,6	6,8	5,2	»
13	289	1,3	16,2	18,0	16,4	22,4	9,4	8,2	»
14	253	—	—	—	—	—	—	—	weak
Average in mm.	334,3	1,86	20,33	17,13	14,99	20,2	7,02	5,63	

TABLE 14. *Campanula rotundifolia No. 298, Åre*
Plants in culture since 1921. Notes taken 1924.

1	220	3,64	7	24,46	21,44	24,8	9,2	5,4	strong
2	310	2,6	7,2	22,64	21,4	25,02	10,6	5,0	weak
3	555	2,6	13,8	23,48	22,4	26,22	9,58	5,8	strong
4	330	2,82	9	21,98	21,2	27,36	8,92	6,2	»
5	350	3,42	22,8	22,6	22,2	26,24	9,66	6,4	»
6	400	2,0	14,6	23,42	21,42	25,84	8,42	5,8	»
7	240	2,82	13,2	19,2	19,3	22,66	7,42	5,4	weak
8	—	—	—	—	—	—	—	—	»
9	230	2,96	5,2	21,52	21,5	26,0	10,0	6,2	strong
10	250	2,46	4	16,66	19,18	22,84	9,98	5,8	»
11	275	2,98	18,8	21,0	20,3	25,42	8,62	6,0	»
12	370	3,8	16	23,18	21,54	28,4	10,4	6,2	»
13	300	3,2	13,2	25,2	20,2	27,5	10,42	6,4	weak
14	325	2,8	15,8	24,98	20,8	27,8	10,7	5,4	strong
15	210	3,22	4,8	17,78	19,5	23,2	8,52	4,6	»
16	330	3,2	10,2	23,24	20,76	26,5	9,46	4,4	»
17	240	2,96	8,4	22,5	22,9	28,8	10,16	9,0	»
Average in mm.	308,43	2,97	11,5	22,12	21,0	25,91	9,54	5,88	

TABLE 15. *Campanula rotundifolia No. 349, Bergen.*
Plants in culture since 1922. Notes taken 1924.

Field number	Length of longest stem in mm.	Width of middle stem leaves	Number of flowers on stems	Length of corolla	Width of corolla in the middle	Width of corolla at mouth	Length of corolla lobes	Length of calyx lobes	Power of regeneration of basal rosette leaves
1	487	1,8	8,6	22,0	24,0	30,6	9,66	6,8	strong
2	385	3,8	13,2	20,38	20,18	25,42	8,6	4,4	weak
3	400	3,0	8,6	19,2	21	25,6	8,4	4,6	strong
4	—	—	—	—	—	—	—	—	»
5	355	2,8	8,4	18,2	17,4	20,6	7,2	6,0	weak
6	330	3,0	8,33	23,0	22,0	28,0	8,0	6,0	»
7	315	1,98	8,0	20,6	18,6	23,8	8,6	4,4	»
Average in mm.	378,67	2,73	9,19	20,56	20,53	25,67	8,41	6,36	

TABLE 16. *Campanula rotundifolia No. 240, Trondhjem.*
Plants in culture since 1922. Notes taken 1924.

1	203	—	—	—	—	—	—	—	—
2	298	2,06	13,6	20,2	19,4	25,4	7,0	6,6	strong
3	273	2,3	11,25	18,8	18,2	25,6	8,6	4,3	»
4	289	—	—	—	—	—	—	—	—
5	393	2,1	22	23,6	18,0	24,4	9,0	5,6	»
6	290	2,34	12,2	18,4	18,6	26,4	8,8	4,2	weak
7	357	—	—	—	—	—	—	—	strong
8	314	2,2	16,2	18,4	17,2	23,4	7,6	5,8	»
9	322	1,8	18,4	21,0	19,2	26,4	7,6	6,0	weak
10	495	1,7	7,6	24,4	18,6	25,0	9,0	8,0	»
11	311	1,96	12,0	21,6	18,8	26,2	9,0	5,8	strong
12	426	2,0	21,2	22,8	18	24,6	9,3	5,9	weak
13	346	—	—	—	—	—	—	—	strong
14	387	1,8	25,2	20,8	17,4	23,2	8,0	5,8	»
Average in mm.	336	2,03	15,97	21,0	18,34	25,06	8,39	5,8	

TABLE 17. *Campanula rotundifolia Nos. 19 and 25, Abisko.* Plants raised from seeds, coll. 1921. Notes taken 1924.

Field number	Length of longest stem in mm.	Width of middle stem leaves	Number of flowers on stems	Length of corolla	Width of corolla in the middle	Width of corolla at mouth	Length of corolla lobes	Length of calyx lobes	Power of regeneration of basal rosette leaves
19,1	—	—	—	—	—	—	—	—	—
2	164	2,0	9,4	22,6	18,3	25,6	8,0	5,3	strong
3	270	1,9	10,0	22,5	18,5	25,0	8,5	8,5	»
4	440	2,06	31,2	23,0	21,0	27,5	9,0	8,0	»
5	266	2,8	8,2	24,6	25,6	31,7	10,3	6,6	»
6	—	—	—	—	—	—	—	—	—
25,1	—	—	—	—	—	—	—	—	—
2	168	1,78	6,4	30,0	22,0	30,0	10,0	8,5	»
3	—	—	—	—	—	—	—	—	—
4	—	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—	—
6	358	1,72	12,0	26,5	19,5	27,5	10,0	8,5	»
7	192	1,6	20,6	24,0	18,5	26,5	9,5	10,0	»
Average in mm.	250,1	1,99	13,97	24,47	20,48	27,68	9,32	7,9	

TABLE 18. *Campanula rotundifolia No. 770, Freiburg.* Plants in culture since 1923. Notes taken 1924.

1	270	2,38	16	22,2	19,6	24,6	8,8	6,0	weak
2	461	2,22	26,0	20,8	18,8	26,8	9,8	6,2	none
3	185	2,00	7,0	20,0	19,24	25,18	8,84	6,4	»
4	429	1,62	47,3	20,0	18,4	23,6	8,0	6,5	weak
5	376	1,24	14,2	21,58	21,14	25,8	8,2	6,4	»
6	230	1,44	11,8	20,2	19,38	24,98	8,0	7,14	»
7	351	2,42	13,0	17,6	18,2	22,6	7,6	6,0	»
8	312	2,18	14,4	23,66	21,4	27,58	9,3	6,6	»
9	386	1,98	8,4	19,98	16,66	20,0	7,56	6,0	»
10	475	3,26	29,0	19,0	18,2	24,8	9,0	5,4	none
11	395	2,8	17,6	22,0	20,2	25,2	9,2	7,8	»
12	511	1,26	27,6	22,5	18,75	25,5	7,75	6,75	»
13	348	2,14	11,0	19,0	15,6	21,2	8,0	6,0	weak
14	330	2,02	16,0	17,8	17,2	23,0	8,2	6,8	none
15	463	2,24	11,6	19,2	18,0	24,8	8,0	6,4	weak
16	535	2,42	46,8	21,5	21,45	27,0	9,8	8,6	»
Average in mm.	378,56	2,12	19,86	20,44	18,89	24,54	8,5	6,56	

TABLE 19. *Campanula rotundifolia No. 796, Feldberg.*
Plants in culture since 1923. Notes taken 1924.

Field number	Length of longest stem in mm.	Width of middle stem leaves	Number of flowers on stems	Length of corolla	Width of corolla in the middle	Width of corolla at mouth	Length of corolla lobes	Length of calyx lobes	Power of regeneration of basal rosette leaves
1	220	3,78	5,6	22,55	21,5	26,0	7,5	7,2	strong
2	205	3,6	5,8	22,8	20,72	26,2	8,95	7,4	»
3	209	4,2	5,2	24,92	22,9	26,8	7,94	7,8	»
4	277	3,64	4,8	19,82	19,9	23,5	7,05	8,0	»
5	185	4,6	10,0	26,0	22,25	27,75	10,0	8,75	»
6	320	4,68	6,0	27,0	24,13	26,0	10,0	—	»
7	150	3,76	6,4	26,6	23,3	26,66	9,2	8,2	»
8	—	5,38	—	—	—	—	—	—	»
9	210	5,44	6,0	25,0	23,9	27,0	—	8,2	»
10	273	3,90	10,0	23,45	21,55	28,0	9,45	7,25	»
11	210	3,84	10,0	21,5	21,0	27,5	—	9,0	»
12	275	6,2	7,0	25,0	28,95	23,1	—	7,6	»
13	245	2,98	6,8	20,22	19,6	22,62	—	7,6	»
14	190	4,0	5,8	20,0	14,0	18,0	—	7,7	»
Average in mm.	224,66	4,29	6,88	23,45	21,82	25,32	8,76	7,89	

15. ECOTYPES OF SOLIDAGO VIRGAUREA L.

The material of *Solidago virgaurea* comprises several hundred individuals transplanted from their natural habitats and now growing in the experimental fields. In the two last years efforts have been made to complete the cultures with extra-Scandinavian material, and series from Germany, the Alps and the Carpathians are now in culture. These series, as well as the series collected in Lappland, are too young to be discussed at present. There remains, however, a number of series from lowland and alpine habitats, which are well suited for the demonstration of changes in the species-population with changes in habitats.

The series to be discussed here come from wooded regions in the southern part of the country (Stenshuvud, Nättraby and Böda on Öland), from the central Scandinavian mountain district (coll. in *Vaccinium myrtillus*-rich forests of Norway spruce on Frösön, at Åre and in *regio subalpina* at about 900 m. sup. m. on Åreskutan), from Bergen and Trondhjem on the west coast of Norway, and from alpine habitats at Finse (coll. in *Anthoxanthum*-meadows at about 1350 m. sup. m.). Table 20 summarizes the average values obtained for some of the characteristics investigated in each of the cultivated series, which are given in tables 21—29. In table 20 (last column) the time of the development of the first flowers, as seen in the cultivated series, is also given.

TABLE 20.

Nos.	Transplanted from	Length of longest stem in mm.	Averagewidth of radiate flowers	Shape of inflorescence	Power of regeneration of basal rosette leaves	Time of first flowers in the cultures
116	Stenshuvud	933	1,91	exp.-spread.	none—weak	latter part of July
602	Nättraby...	889	1,77	»	none	»
683	Böda.....	765,30	1,60	»	none—weak	»
277	Frösön.....	567,20	2,02	contr.-exp.	none—strong	latter part of June
296	Åre	556,80	2,28	contr.-spread.	»	»
382	Åreskutan	458,80	2,35	contracted	mostly strong	middle of June
346	Bergen.....	632,30	2,01	contr.-spread.	mostly none	»
238	Trondhjem	588,27	1,81	contr.-exp.	none—weak	»
364	Finse	384,80	2,12	contracted	mostly strong	first part of June

The values given for each individual in tables 21—29 are average values based upon measurements or countings of five leaves, five

heads (column 5) and five radiate flowers in five different heads (not terminal ones) of each individual.

Fig. 38 shows dried specimens of the Finse type from its natural habitat. It has an average height of about 100 mm., although plants somewhat taller and lower in stature are also found. The height increases considerably in culture and already after one year's cultivation measures about three times the original height. The height now attained does not change in the following year in the direction of a general increase. On the contrary, the height fluctuates within narrow limits so that an individual of a certain height in 1923 might become a trifle lower in stature in 1924, and vice versa. All the individuals, however, show a powerful increase in bulkiness; from being a one-stemmed pygmy in the year of transplantation a bulky block of up to 20 flowering stems may become developed in the course of two years' cultivation. Fig. 39 pictures three individuals of this series as seen in the cultures in 1924. The plant in the middle represents the average height, the plant to the right is the only one in the series which has attained this exceptional height (542 mm.). Beside the low stature of growth the cultivated Finse type shows a number of other characteristic features. The heads are large and usually single on the short branches forming a dense and uninterrupted thyrsus. The ray-flowers are also wider than in the lowland type (see tables). In addition, the power of leaf-regeneration at the base of the stem is very marked. The type is also the earliest among the

Fig. 38. *Solidago virgaurea.* Dried and mounted plants coll. at Finse. The plant on the upper right hand corner 110 mm.

cultivated series; the flowering period begins as early as the first part of June.

The series from the central Scandinavian mountain district have all as large heads as the Finse type and are all considerably lower in stature and earlier than the lowland series. The subalpine series from Åreskutan, however, is somewhat more extreme and shows more resemblance to the Finse series, particularly with regard to the contracted and dense inflorescence and with respect to the power of leaf-regeneration during the flowering period. This series is also considerably lower in stature than the two other series. The lower stature and the powerful leaf-regeneration of the Åreskutan

Fig. 39. *Solidago virgaurea*, cult. individuals of the alpine type from Finse (cf. fig. 38).

series is clearly seen in figs. 40 and 41, where two plants of each series from Åreskutan and Frösön are shown. The individuals of the former series have also very much broader ray-flowers than the two other series. The increase in extremeness of type with the extremeness in habitat conditions exhibited in these series illustrates in an interesting way the changes in the composition of the population which must have taken place in response to the varying habitat conditions at different points within the area of distribution. The significance of the changes will be further discussed in the following pages.

It should be added that the Åreskutan individuals are often considerably lower in stature while growing in their natural habitat. The behaviour of these individuals when cultivated is similar to that already described in the case of the Finse dwarfs. They increase in

height already after one year's cultivation and keep the height then attained in the following years with but very slight fluctuations.

When the alpine and subalpine types of the species are compared with the lowland material (Nos. 116, 602 and 683; see tables) important differences are at once seen. The lowland plants are considerably taller, the inflorescence is branched and therefore expanding or spreading, the power of leaf-regeneration at the base when flowering is none or weak and flowering does not begin until the latter part of July. Further, the heads are much smaller than in the above series. Fig. 42 gives a good idea of the habitus of lowland plants (from Stenshuvud) when cultivated.

Fig. 40. *Solidago virgaurea.* Cult. individuals of the subalpine type from Åreskutan.

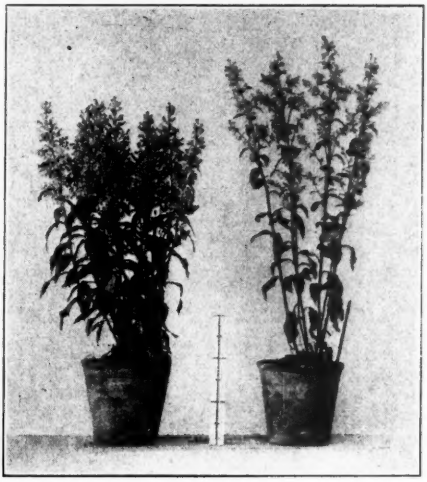

Fig. 41. *Solidago virgaurea.* Cult. individuals from Frösön.

As to the series transplanted from the west coast of Norway (Nos. 238 and 346) an examination of the table records will show these series to be very mixed. This species thus behave much in the same way as other species mentioned before, the different types of which, on account of the close proximity of the mountains to the sea, meet and hybridize here.

In order to demonstrate the differences in leaf shape between different types leaves from representative, cultivated individuals have been mounted and given in figs. 43—50. The lower cauline leaves of the lowland plants are all acuminate and taper into a rather

long tip (figs. 43 and 44). The material of the central Scandinavian mountain district (figs. 45, 46 and 47) has the cauline as well as the radical leaves acute and less tapering at the apex. The leaves of the Finse type (fig. 48) are more narrow, acute and have longer petioles. The series of the Norwegian west coast comprise different types of leaves, as is seen from figs. 49 and 50.

It should also be mentioned that the leaves of the alpine and

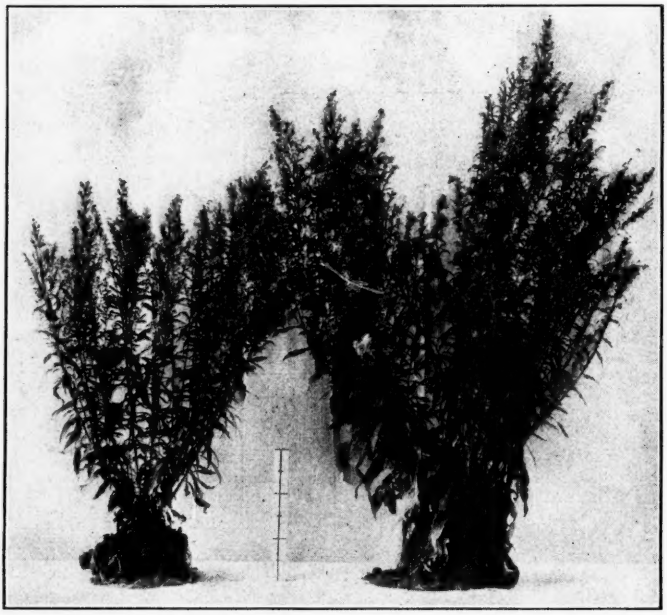

Fig. 42. *Solidago virgaurea.* Cult. individuals of the southern lowland type.

boreal material have throughout been found to be thicker than the leaves of the lowland material.

As to the exhaustive grouping of the species-population into ecotypes much more extensive cultures than the present ones are needed before any conclusive results can be attained. The lowland material especially has to be much increased. The lowland type (probably including several edaphic ecotypes) of southern Sweden reaches down in Germany, as cultivated material tends to show, but it is supplanted by another type in the southern parts of Germany, which type again in the Alps is supplanted by others. The population found on

Frösön and at Åre represents in all likelihood the more northernly type, while the type now in culture from Lappland seems to be identical with the type brought home from Åreskutan.

The latter type will be designated here as the *subalpine ecotype* of the species. It has probably its main distribution in *regio subalpina,* and is no doubt very common in the Scandinavian North. As far as can be judged from the cultivated material brought home from the subalpine region of the Alps no marked differences exist between this material and the subalpine Swedish material. The extreme type transplanted from *regio alpina* in Finse is designated here as the *alpine ecotype* of the species. As to the geographical distribution of this ecotype nothing can be said at present. It occurs probably, in other places in the alpine region of Scandinavia, at least in Norway. My material from different localities in the Alp range does not include any series from *regio alpina.*

A few words should be said as to the systematization of the different types in the floristic handbooks. An extreme alpine form has been distinguished, viz. var. *arctica* HARTM., which, according to SIMMONS (1907), is synonymous with *Solidago minuta* L., *S. lapponica* WITH. and with the var. *alpestris* of REICHENBACH. The diagnosis of this form given by SIMMONS (l. c.) does not cover our alpine ecotype, neither in a cultivated state, nor in its habitat modification. — The type designated here as the subalpine ecotype might be the *S. virgaurea* var. *alpestris* (W. and K.) DC in the above mentioned paper by SIMMONS. This variety, according to SIMMONS, grows also in the subalpine region of the Alps as well as that of the Carpathians. According to my own findings, however, the subalpine type of the Alps, while probably identical with the Scandinavian, is not identical with the subalpine type of the Carpathians. To these questions more attention will be paid on a later occasion. The question will then also be discussed as to whether or not the alpine dwarf of our systematic handbooks (var. *arctica* HARTM., now called var. *minuta* (L.) SIMM.; also synonymous with var. *pumila* (WILLD.) GAUDIN of German manuals) is a habitat modification of the var. *alpestris* (W. and K.) DC. It must suffice here to state that the var. *minuta* (= var. *pumila*) in all probability includes forms genotypically lower in stature then the forms of lower regions as well as merely habitat dwarfs (modifications), and that therefore the plant by one author might represent a hereditary variation, by another author merely a modification. Cultivation alone is able to settle the question.

TABLE 21. *Solidago virgaurea No. 116, Stenshuvud.*
Plants in culture since 1920. Notes taken 1924.

Field number	Length of stem in mm.	Length of longest inflorescence in mm.	Shape of inflorescence	Average number of radiate flowers in head	Length of radiate flowers	Width of radiate flowers	Length of basal stem leaves	Width of basal stem leaves	Power of regeneration of basal rosette leaves
1	990	650	expanded-spreading	10,2	5,0	2,2	80,5	25,0	none
2	1070	720	»	7,5	6,4	2,0	76,4	20,2	»
3	850	490	spreading	8,5	4,8	1,6	90,5	30,5	»
4	990	580	»	10,0	5,0	2,0	88,0	35,0	»
5	880	500	»	9,0	4,5	2,0	75,5	25,2	»
6	1100	700	»	7,2	5,0	1,8	100,0	40,2	weak
7	870	620	expanded-spreading	10,2	6,0	2,0	98,2	35,5	»
8	850	520	»	8,4	5,5	2,2	102,0	42,0	none
9	820	480	»	10,0	4,5	1,5	95,5	40,5	weak
10	910	540	»	9,2	5,0	1,8	100,2	35,0	»
Average in mm.	933	580		9,02	5,17	1,91	90,68	32,91	

TABLE 22. *Solidago virgaurea No. 602, Nättraby.*
Plants in culture since 1923. Notes taken 1924.

1	1030	950	spreading	11	6,2	1,8	111,2	35	none
2	1100	910	expanding	10	6,5	2,0	126	30	»
3	970	760	»	11	7,0	1,9	136,2	27,7	»
4	880	700	»	9,4	6,8	2,2	115	31	»
5	1000	920	»	8,0	5,7	1,8	130	23,5	»
6	1020	820	»	10,2	6,7	1,4	145	35	»
7	—	—	—	—	—	—	115	30	»
8	920	710	expanded-spreading	9,0	6,9	1,8	101	22,6	»
9	900	600	»	9,2	6,4	1,5	106	26	»
10	820	660	spreading	8,4	6,4	1,7	122	28,2	»
11	800	490	»	9,2	6,2	1,8	114	25,5	»
12	650	520	»	8,3	5,6	1,3	127,6	30,4	»
13	870	660	»	10,0	5,4	2,0	132,5	32,4	»
14	600	400	»	—	—	—	—	—	—
Average in mm.	889	700		9,55	6,31	1,77	121,70	29,01	

TABLE 23. *Solidago virgaurea No. 683, Böda.*
Plants in culture since 1923. Notes taken 1924.

Field number	Length of stem in mm.	Length of longest inflorescence in mm.	Shape of inflorescence	Average number of radiate flowers in head	Length of radiate flowers	Width of radiate flowers	Length of basal stem leaves	Width of basal stem leaves	Power of regeneration of basal rosette leaves
1	930	630	expanded-spreading	10,0	4,4	1,6	104,0	24,0	none
2	700	550	»	11,5	5,0	1,8	108,5	38,2	»
3	680	540	»	8,4	4,8	2,0	110,2	35,4	»
4	—	—	—	—	—	—	—	—	—
5	840	520	spreading	8,8	4,2	1,3	112,5	28,2	»
6	700	550	expanded-spreading	9,5	5,0	1,5	115,3	25,0	»
7	670	450	»	10,0	6,0	2,0	102,0	26,2	»
8	800	560	»	9,4	4,6	1,8	100,0	30,5	weak
9	650	480	expanded	8,2	5,2	1,6	120,4	42,4	»
10	870	570	»	9,5	4,3	1,5	108,5	28,2	none
11	750	550	»	11	5,0	2,0	140,0	30,4	»
12	950	600	»	10,0	4,6	1,8	122,0	26,5	»
13	610	400	»	8,5	5,2	2,1	115,0	28,5	weak
14	670	500	»	9,0	4,8	1,6	120,5	25,0	none
15	820	620	»	10,0	5,5	2,0	138,0	32,0	»
16	840	580	»	8,6	4,4	1,7	124,5	20,5	»
Average in mm.	765,30	540		10,17	4,56	1,60	116,09	29,44	

TABLE 24. *Solidago virgaurea No. 277, Frösön.*
Plants in culture since 1921. Notes taken 1924.

1	490	423	contracted	12,8	8,56	2,2	104,2	36,0	strong
2	534	329	»	11,6	7,58	2,14	85,2	24,4	none
3	371	338	»	10,6	8,08	2,04	76,4	26,4	»
4	522	306	»	9,8	8,02	2,36	66,6	30,4	weak
5	614	373	»	10,0	7,8	2,12	80,2	29,5	none
6	483	317	»	9,8	7,7	2,2	84,8	27,2	»
7	664	342	»	11,0	7,3	2,06	75,0	28,2	strong
8	568	399	»	10,0	7,44	2,16	87,0	30,2	weak
9	503	404	expanded	10,6	6,6	1,94	78,6	25,6	none
10	782	441	»	10,6	7,32	1,6	77,0	27,5	weak
11	623	416	contracted-expanded	10,6	6,9	1,72	82,3	26,7	none
12	762	412	»	10,2	7,26	1,7	79,8	26,6	»
13	530	391	»	10,8	7,18	1,5	75,6	26,8	»

Field number	Length of stem in mm.	Length of longest inflorescence in mm.	Shape of inflorescence	Average number of radiate flowers in head	Length of radiate flowers	Width of radiate flowers	Length of basal stem leaves	Width of basal stem leaves	Power of regeneration of basal rosette leaves
14	632	368	contracted	14,4	6,00	1,82	83,4	23,4	weak
15	618	354	»	10,4	6,38	2,12	88,2	30,6	»
16	607	475	»	8,6	6,64	1,9	120,6	39,8	none
17	304	274	contracted-expanded	10,8	7,14	2,78	—	—	»
18	603	318	contracted	11,2	6,84	1,92	88,8	25,4	weak
Average in mm.	567,20	371,10		10,76	7,26	2,02	79,7	26,9	

TABLE 25. *Solidago virgaurea No. 296, Åre.*
Plants in culture since 1921. Notes taken 1924.

1	689	530	spreading	11,6	6,68	2,26	123,8	35,6	none
2	538	367	contracted	7,6	8,5	2,52	85,6	26,0	weak
3	544	398	spreading	10,4	9,42	2,4	63,4	23,8	none
4	606	528	contracted	12,0	7,4	2,0	105,0	37,2	»
5	547	405	»	10,4	9,78	2,38	96,2	29,0	strong
6	537	463	»	12,8	7,4	2,94	92,0	33,8	weak
7	461	319	»	11,0	7,58	2,48	91,4	27,0	strong
8	563	436	»	10,8	7,9	2,12	88,4	38,0	none
9	488	347	»	9,8	8,96	1,94	87,0	24,4	weak
10	572	404	»	11,0	7,38	2,08	77,6	34,6	»
11	570	382	»	13,0	6,18	1,9	110,4	30,2	strong
12	322	249	»	11,0	8,84	2,02	43,4	17,2	none
13	578	497	»	11,2	8,98	2,08	91,0	30,4	strong
14	664	504	spreading	11,6	7,0	2,22	99,8	36,4	none
15	650	472	contracted	10,8	8,16	1,94	95,4	39,0	weak
16	611	349	»	11,6	8,36	2,22	82,2	34,7	»
17	523	353	»	9	7,3	1,94	93,4	31,2	strong
18	480	368	»	9,4	8,28	2,74	98,6	40,0	»
19	589	420	»	11,8	8,12	2,42	89,8	34,2	»
20	663	367	»	9,6	8,2	2,48	95,2	41,2	weak
21	588	400	»	10,2	8,58	2,26	99,2	33,2	none
22	575	366	»	10,6	7,94	2,54	83,0	36,0	strong
23	530	486	»	12,4	7,76	2,4	90,2	25,0	none
24	474	413	»	11,6	8,56	2,4	81,4	31,4	»
Average in mm.	556,80	409,3		10,9	8,05	2,28	90,14	32,06	

TABLE 26. *Solidago virgaurea No. 382, Åreskutan 900 m. sup. m.* Plants in culture since 1921. Notes taken 1924.

Field number	Length of stem in mm.	Length of longest inflorescence in mm.	Shape of inflorescence	Average number of radiate flowers in head	Length of radiate flowers	Width of radiate flowers	Length of basal stem leaves	Width of basal stem leaves	Power of regeneration of basal rosette leaves
1	456	318	contracted	10,8	9,24	2,82	113,4	40,8	strong
2	474	301	»	11,8	7,8	2,7	105,8	46,6	weak
3	573	418	»	12,6	9,8	2,06	96,4	32,6	strong
4	485	403	»	12,2	7,74	2,4	77,8	27,0	weak
5	451	243	»	14,5	8,0	2,12	88,6	29,0	strong
6	488	435	»	10,2	9,8	2,24	124,6	44,6	»
7	364	207	»	—	—	—	80,7	25,0	»
8	433	367	»	10,8	7,76	2,52	96,0	32,0	»
9	549	376	»	10,4	9,8	2,1	99,2	30,2	»
10	452	305	»	9,4	9,16	2,3	84,8	25,8	»
11	—	—	»	—	—	—	86,0	32,5	»
12	388	283	»	11,0	9,6	2,16	105,0	33,2	»
13	451	428	»	11,2	7,34	2,46	77,3	26,0	»
14	400	262	»	—	—	—	—	—	»
Average in mm.	458,80	334,3		11,35	8,76	2,35	88,2	30,4	

TABLE 27. *Solidago virgaurea No. 346, Bergen.* Plants in culture since 1922. Notes taken 1924.

1	822	583	spreading	—	—	—	107,4	24,2	none
2	564	344	contracted	8,0	7,04	1,74	93,6	20,8	»
3	748	520	spreading	7,8	6,36	1,88	122,6	44,2	»
4	732	560	expanded	10,6	7,3	2,44	119,0	25,6	»
5	626	512	spreading	8,0	6,16	1,96	107,4	21,4	»
6	568	436	contracted	7,2	5,24	2,18	92,3	25,7	weak
7	631	447	»	10,0	6,08	1,54	86,8	20,8	none
8	689	443	expanded	8,4	6,5	2,12	77,2	34,2	»
9	527	390	contracted	11,4	6,9	2,28	85,2	22,8	»
10	602	334	expanded	9,2	7,58	2,22	84,2	28,0	»
11	483	374	contracted	11,0	5,82	2,52	75,4	26,4	strong
12	584	457	»	8,2	6,08	2,04	84,0	21,8	none
13	720	532	»	9,4	5,58	1,94	84,2	24,4	»
14	539	469	»	7,8	6,72	2,08	73,2	22,6	»
15	638	381	»	9,0	8,34	2,06	96,6	26,6	»
16	665	427	expanded	—	—	—	85,0	32,0	»
17	561	379	contracted	8,2	7,74	1,74	88,0	20,3	»

Field number	Length of stem in mm.	Length of longest inflorescence in mm.	Shape of inflorescence	Average number of radiate flowers in head	Length of radiate flowers	Width of radiate flowers	Length of basal stem leaves	Width of basal stem leaves	Power of regeneration of basal rosette leaves
18	614	431	contracted	9,6	7,1	1,98	95,0	25,4	none
19	766	573	spreading	—	—	—	95,6	26,6	»
20	557	410	contracted	8,2	4,9	1,44	107,3	28,2	»
21	642	441	expanded	6,2	4,68	2,08	87,4	27,8	»
Average in mm.	632,30	449,70		8,79	6,47	2,01	92,73	26,2	

TABLE 28. *Solidago virgaurea No. 238, Trondhjem.*
Plants in culture since 1922. Notes taken 1924.

1	598	312	contracted	11,2	6,6	2,06	74,1	23,0	none
2	697	487	expanded	7,2	6,5	1,8	91,0	26,8	weak
3	655	511	»	8,2	6,52	2,14	107,7	24,8	none
4	619	484	contracted-expanded	6,6	6,3	1,7	101,6	35,6	weak
5	438	286	»	10,6	6,64	1,86	63,2	21,8	none
6	592	385	contracted	8,6	6,42	1,6	81,8	21,2	»
7	439	330	»	8,4	7,62	1,62	55,8	16,6	weak
8	648	482	»	8,8	6,42	1,8	78,4	26,0	none
9	728	603	»	8,2	6,46	2,08	84,2	28,8	»
10	583	364	»	7,8	6,44	2,02	73,4	22,4	»
11	506	344	»	8,2	7,3	1,88	50,6	19,2	»
12	671	519	expanded	8,4	6,08	1,22	121,2	28,6	weak
13	615	408	contracted	9,4	6,76	1,34	68,0	22,6	none
14	522	407	expanded	8,6	7,5	2,06	71,2	18,6	weak
15	513	413	»	7,6	7,44	1,9	71,2	19,8	»
Average in mm.	588,27	422,33		8,52	6,73	1,81	79,6	23,7	

TABLE 29. *Solidago virgaurea No. 364, Finse.*
Plants in culture since 1922. Notes taken 1924.

1	385	273	contracted	10,4	6,34	2,28	92,0	19,4	strong
2	542	281	»	9,8	3,94	2,12	—	—	»
3	456	268	»	9,0	6,28	2,06	99,6	20,6	»
4	472	347	»	9,4	6,22	1,96	94,6	23,8	»
5	503	317	»	11,4	5,9	2,1	76,0	15,0	»

Field number	Length of stem in mm.	Length of longest inflorescence in mm.	Shape of inflorescence	Average number of radiate flowers in head	Length of radiate flowers	Width of radiate flowers	Length of basal stem leaves	Width of basal stem leaves	Power of regeneration of basal rosette leaves
6	388	252	contracted	8,4	7,2	2,08	68,2	18,8	strong
7	408	239	»	10,4	5,9	2,3	84,0	19,4	»
8	—	—	—	9,0	5,41	2,52	77,0	21,0	»
9	371	288	»	7,0	5,82	1,84	64,8	15,2	»
10	340	226	»	10,4	6,62	2,08	84,0	18,7	»
11	374	193	»	10,4	6,0	1,98	68,2	14,5	»
12	313	204	»	10,6	6,58	2,36	68,0	16,0	»
13	443	220	»	11,6	5,7	2,02	93,2	18,0	»
14	394	231	»	10,2	5,38	2,06	78,0	13,6	»
15	396	303	»	11,2	5,7	2,0	73,5	12,5	»
16	304	282	»	10,8	6,16	2,36	81,0	18,0	weak
17	295	223	»	10,8	6,14	2,44	69,8	14,2	strong
18	426	312	»	9,6	6,78	2,18	79,8	15,4	weak
19	276	219	»	9,0	5,64	2,04	75,0	16,6	strong
20	352	261	»	9,8	7,18	2,14	90,0	15,4	»
21	438	306	»	11,8	6,52	2,04	73,0	13,2	»
22	406	247	»	10,2	6,44	2,08	81,6	16,8	»
23	258	221	»	13,6	6,02	2,0	90,2	20,6	»
24	310	213	»	12,2	6,08	1,92	91,2	19,0	»
Average in mm.	384,80	257,70		10,29	6,08	2,12	80,60	17,2	

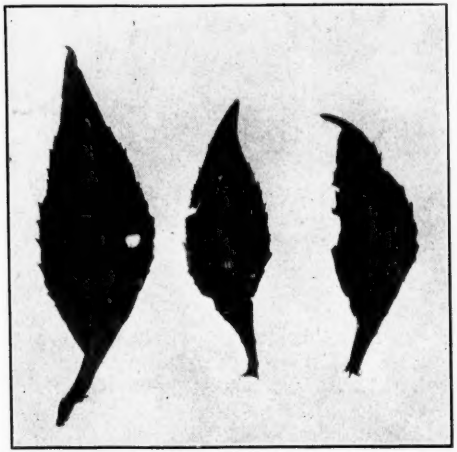

Fig. 43. Lower cauline leaves of the cult. lowland type.

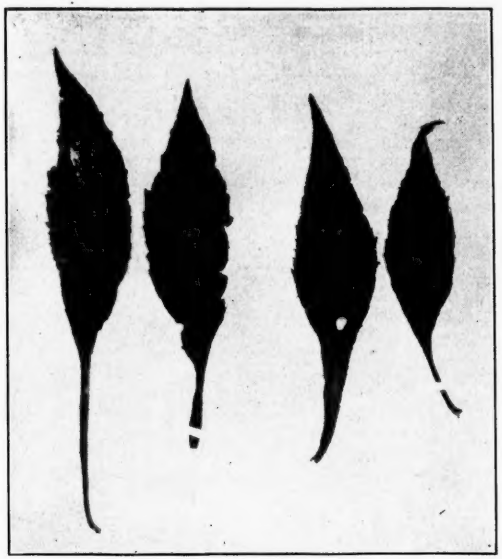

Fig. 44. Lower cauline leaves from two individuals of the cult. lowland type.

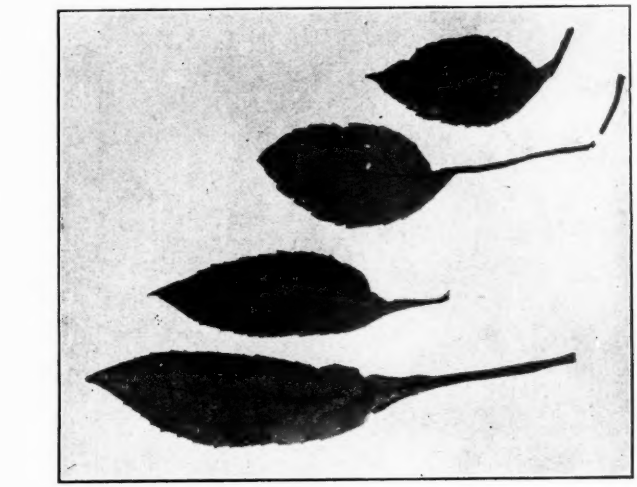

Fig. 46. Radical and cauline leaves from two individuals of the cult. type from Åre.

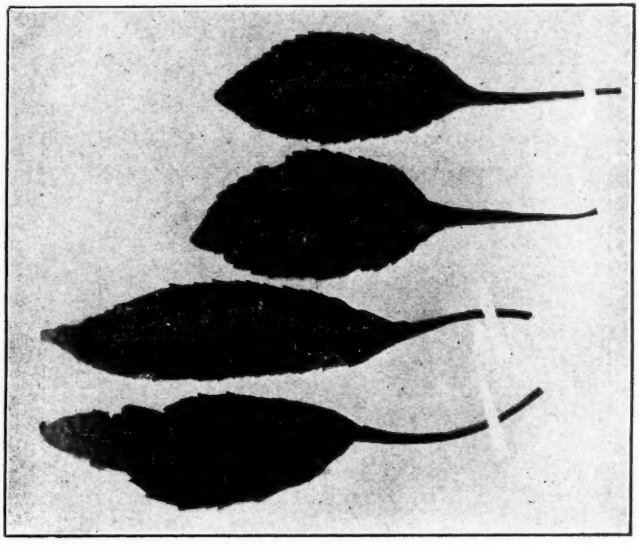

Fig. 45. Radical leaves of the cult. type from Frösön. Two different individuals.

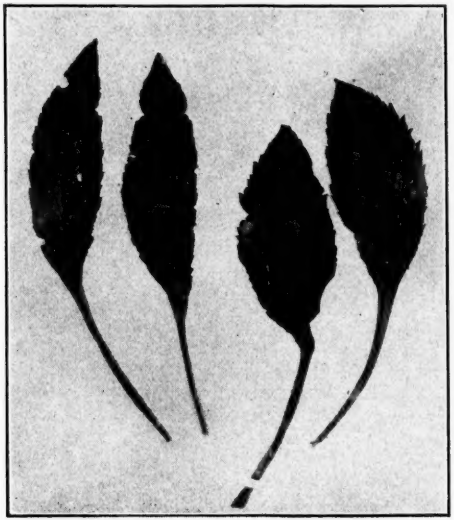

Fig. 47. Radical leaves of two individuals of the cult. subalpine type from Åreskutan.

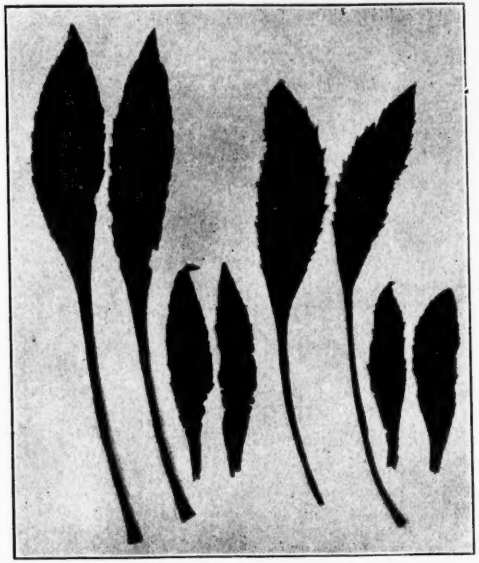

Fig. 48. Radical and cauline leaves of two individuals of the cult. alpine type from Finse.

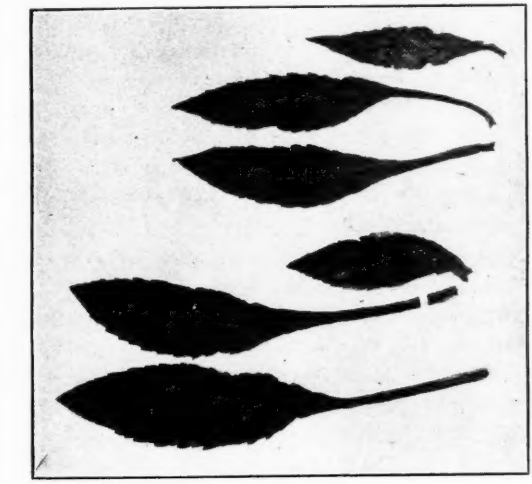

Fig. 50. Radical and cauline leaves of two individuals of the cultivated Bergen series.

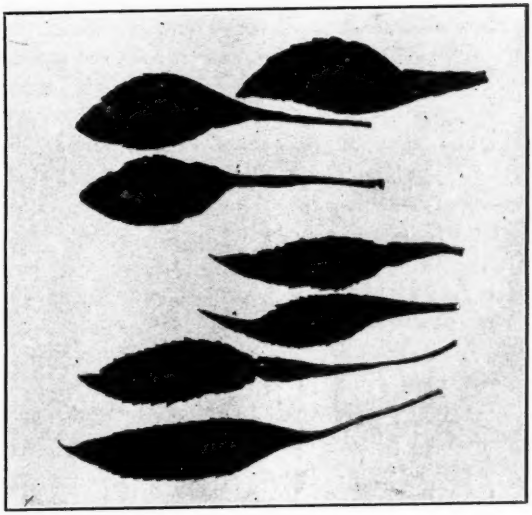

Fig. 49. Radical and cauline leaves of two individuals of the cultivated Trondhjem series.

II. THE DIFFERENTIATION OF PARALLEL ECOTYPES IN DIFFERENT SPECIES.

It has been known for quite a long time that plants distant in affinity but inhabiting the same habitat may also show one and the same, or similar, growth-forms (life-forms). Our handbooks in ecology and plant-geography usually explain the thing by taking refuge to »epharmonic convergence» (e. g. WARMING 1909 b), an expression duly criticised by JOHANNSEN (1913, p. 430). The Lamarckian view expressed in such terms received undue consideration when it was found by experiments that structural characteristics typical of plants of extreme habitats (saline soils, alpine situations, etc.) could be modificatorily induced in non-halophytes, in lowland plants, etc. These questions have been discussed and enlarged upon in a previous paper (TURESSON 1922). At the same time as it was pointed out there that the Lamarckian view of the origin of the hereditary habitat types dealt with could not possibly be held, it was shown, that habitat types, hitherto thought to be merely modifications, were of a hereditary nature. Indeed, habitat modifications were rarely met with, the course taken by the plant being instead a genotypical differentiation of the species-population into different hereditary habitat types. However, the general view held by writers on ecology as to similarity in growth form shown by different species when inhabiting less extreme habitats is that this growth form is merely a modification induced by the modificatory action of the habitat factors, while the similarity in the growth form of plants inhabiting very extreme habitats is held to be hereditary in nature, In view of the facts presented in this as well as in my previous papers on the topic this distinction seems worthless with regard to the majority of habitat types.

Nevertheless, the parallel development as to the growth-forms and habitat types of species living in the same habitat is a most interesting problem. In considering at first the Alfvar type on Öland it has already been pointed out that certain characteristics are found to distinguish these types from other types of the same species, viz. extreme prostrateness of the stems (*Artemisia campestris, Rumex acetosella, Silene maritima*) or, in species with other morphology, dwarfishness (*Allium Schoenoprasum*) or much depressed foliage (*Leontodon autumnalis*). There are also other characteristics such as glaucousness (*Allium*), thickness of outer epidermis walls (*Arte-*

misia) and isolaterality *(Leontodon).* Similar xerophytic »adaptations» have been found typical of the Alfvar types of various grasses (see a forthcoming paper by Mr. E. HELLERSTRÖM). That these characteristics, formerly thought to be purely modifications (GREVILLIUS 1896, p. 28) are hereditary in nature seems superfluous to reiterate at this stage. The prostrate form of *Hieracium umbellatum* described previously (type b in TURESSON 1922, p. 295) seems also to belong here.

The parallel course of type differentiation, which plants inhabiting this habitat exhibit, is beautifully seen within several habitus groups. Plagiotropy of the stems is not only found in *Artemisia, Rumex* and *Silene* but also in the cultivated material of *Centaurea jacea* from the Alfvar, not discussed here. Within the groups of rosette plants the cultivated types show much depressed foliage (cf. TURESSON 1919). This is not only seen in *Leontodon,* but occurs also in other species of this group, for instance in *Plantago maritima,* the Alfvar type of which is easily distinguished in culture from other types of the species by this very characteristic [1]. The lower stature of growth in *Allium,* as well as the glaucousness, is repeated by the Alfvar types of certain grasses, as will be shown later on by Mr. HELLERSTRÖM.

That the above mentioned hereditary features, characteristic of the Alfvar types, are of such a nature, as to indicate a specialisation of these types to the habitat would be a difficult task to deny. The question, however, may be put to the test by applying the principle already formulated (TURESSON 1922, p. 340) as a proof of the essentiality of characters, viz. the parallelism between the modification and the hereditary variation. The dominating habitat factors of the Alfvar, according to WITTE (1906 b), are low water contents of the substratum, strong insolation, strong winds and low atmospheric humidity. The modificatory action of these factors in the direction of dwarf growth, plagiotropy, thick cuticle, isolaterality, etc. are too well known to be discussed here at any length. When it is now found that habitats, where such factors prevail, which by experi-

[1] The statement made by WITTE (1906 a) that the Alfvar form of *P. maritima* develops into »typical» *P. maritima,* when cultivated, is not correct. Certain characteristics, e. g. the dwarfishness, disappear, while other characteristics, e. g. the depressed rosette leaves, are retained in cultivation. When cultivated side by side with series collected in other habitats (coast series from different points, salt steppe series from Hungary, etc.) the differences in this, as well as in other respects, are at once seen.

ments have been found to induce modificatory dwarfishness, plagiotropy, isolaterality, etc., are inhabited by forms in which these very same characteristics are hereditary, no doubt remains as to the essentiality of the characteristics in question, It also illustrates, Lamarckian ideas being untenable, the sorting and controlling effect of the habitat factors, which cause only those individuals of the population to remain, which already »from birth» carry the genotypical constitution necessary to support life in a certain habitat. Another proof of the essentiality of the characteristics found in the hereditary Alfvar habitat types is furnished by the fact that a great number of species making up the Alfvar vegetation are characterised by precisely the same features found to be typical of the hereditary habitat types, viz. dwarfishness, plagiotropy, isolaterality, etc. (see ERIKSON 1895, GREVILLIUS 1896, WITTE 1906 b). These species, in other words, do not occur at present in any other form.

Some of the most important habitat factors prevailing on the Alfvar on Öland are also found to dominate other xerophilous lowland formations, viz. certain types of steppes, heaths and stationary dunes. Thus it is to be expected that types similar to or identical with the Alfvar types may be found in these habitats. The extremely prostrate type of *Hieracium umbellatum* on the stationary dunes of eastern Scania, already alluded to, is undoubtedly a case in point. Other cases are under investigation.

When it is thus seen that within similar habitus groups of species similar hereditary habitat types become differentiated as a result of the sorting and controlling effect of definite habitat factors upon the species populations, and when it is further seen that, as a result of the same controlling effect, the habitat types of the different habitus groups all show characteristics which indicate a specialisation to one and the same habitat, a uniform naming of such habitat types becomes of great importance both to ecology and systematism. Accordingly, I propose that the hereditary habitat type differentiated within species of different habitus (renascent herbs, broad leafed rosette plants, grasses, etc.) in genotypical response to the habitat factors of the Alfvar and ecologically similar formations be designated as oecotypus *campestris*.

The habitat types of the mobile dunes represent another interesting group although much remains to be done before the characteristics of these types become recognised. However, I have already described such a type of *Hieracium umbellatum* from the drift-sand

and white dunes along the western coast of Sweden and in the Sandhammar region (type a in TURESSON 1922, p. 295). It has stems less prostrate than in *H. umbellatum* oect. *campestre,* while the power of shoot-regeneration is much more powerful. The type is confined to the dunes as is shown by a closer investigation of the population at the edges of the dune regions (l. c. p. 331—332). Such dune types of *Hieracium umbellatum* will certainly be found also in other places. In order to compare the dune types found in Sweden with the types in the extreme sand-dune region of West-Jutland in Denmark material of a number of species has been brought in culture from different points within that region. The material is too young, however, to allow any conclusions to be drawn just yet. In the Swedish dune material the shifting dune type of *Artemisia campestris* described in this paper is worth noting. Hereditary types from mobile dune habitats are also found within other habitus groups. *Festuca rubra* var. *arenaria* (OSB.) FR. is such a type, in which the dangers of sand-covering is minimised by fast-growing stolons, which in this type are more numerous and longer than in the other types of *Festuca rubra* (cf. RAUNKIÆR 1895—1899, p. 557). Cultivated material of this type has shown these characteristics to be of an undubitable hereditary nature, and investigations in nature show that the type on the border of the dune regions hybridises with other types of the species and is supplanted in other habitats by such types (so, for instance, on Hallands Väderö, where the dunes on the east side of the island harbour the *arenaria* type, which is then supplanted to the north and south, where cliffs replace the dunes, by a type much like subsp. *tenuifolia* HOWARTH; cf. HOWARTH 1921). Shifting dune types are found in still other habitus groups, in *Viola tricolor* for instance, where the var. *maritima* SCHWEIGG., of an undoubtedly hereditary nature (CLAUSEN 1922) by means of powerful shoot-regeneration is able to hold its own in the mobile sand (cf. WARMING 1909 a, p. 227).

I here propose that the hereditary types, which have become differentiated within different species and habitus groups in genotypical response to the shifting dune habitat, be grouped into oecotypus *arenarius.*

The habitat types characteristic of saline soils show much uniformity as to the fleshiness of the leaves. These types have been dealt with in detail in a previous paper (TURESSON 1922), and others (in *Lythrum salicaria* and *Plantago major*) have been described in

the present paper. So far only types from the coast have been investigated. However, investigations are at present being made which also aim at throwing light upon the saline habitat types of the salt steppes of continental Europe. Meanwhile, the group of hereditary habitat types of non-halophytic inland species which has become differentiated in response to saline habitats is here designated as oecotypus *salinus*.

The ecotypical nature of alpine and subalpine forms has been discussed in detail in the present paper. It has been shown that these types show much resemblance to plant species entirely limited to alpine and arctic regions, for instance, as regards thickness of leaves, dwarfishness, caespitous growth and earliness (cf. KJELLMAN 1884 and SCHIMPER 1908). That the characteristics shown by the alpine and subalpine habitat types are of the nature of »adaptations» cannot be denied when it is remembered that similar characteristics are readily induced modificatorily in lowland plants when transplanted in alpine habitats (KERNER 1891, BONNIER 1895). The differences in extremeness of the characteristics, especially with regard to stature, between the alpine and subalpine types should also be noted. In accordance with the facts adduced in this paper the group of hereditary types, differentiated within lowland species of different habitus as the result of the sorting and controlling effect of subalpine habitat factors upon the genetically heterogeneous species-populations, is designated as oecotypus *subalpinus*.

Similarly the hereditary habitat type differentiated within lowland species of different habitus in genotypical response to the habitat factors of *regio alpina* is designated as oecotypus *alpinus*.

In the following list the species differentiated into the hereditary habitat types discussed above and in my previous paper (TURESSON 1922) are put together into respective ecotype groups. In order to bring out the great variety of names given to these types (in their habitat modifications) the systematical names are also given. It has already been pointed out that some of the habitat types have escaped the observation of systematists.

Oecotypus *campestris*:

Allium Schoenoprasum
Artemisia campestris
Centaurea jacea f. *humilis* SCHRANK.
Hieracium umbellatum f. *dunense* REYN., f. *humile* SCHUM., etc.

Leontodon autumnalis	var. *coronopifolius* LGE.
Plantago maritima	f. *lanigera* K. JOH.
Rumex acetosella	f. *angustifolius* KOCH.
Silene maritima	f. *petræa* FR.

Oecotypus *arenarius*:

Artemisia campestris	var. *sericea* FR.
Festuca rubra	var. *arenaria* (OSB.) FR.
Hieracium umbellatum	f. *filifolium* FR. (?)
Viola tricolor	var. *maritima* SCHWEIGG., etc.

Oecotypus *salinus*:

Armeria vulgaris	*A. maritima* (MILL) WILLD.
Hieracium umbellatum	
Leontodon autumnalis	f. *salinus* ASPEGR.; f. *robustior* NEUM.
Lythrum salicaria	
Matricaria inodora	var. *maritima* (L.).
Melandrium rubrum	var. *crassifolium* FR.
Plantago major	f. *scoparia* FR.
Solanum dulcamara	var. *marinum* BAB.
Spiræa ulmaria	

Oecotypus *alpinus*:

Geum rivale	f. *humile* SCHUR. (?)
Leontodon autumnalis	f. *taraxaci* (L.).
Melandrium rubrum	var. *subacaulis* NORM. (partly).
Myosotis silvatica	
Ranunculus acer	f. *pumilus* (auct.)
Rumex acetosa	
Solidago virgaurea	var. *arctica* HARTM. (?)

Oecotypus *subalpinus*:

Campanula rotundifolia	var. *Gieseckiana* (VEST) SIMM. and subsp. *Scheuchzeri* VILL.
Geum rivale	f. *subalpinum* NEUM.
Melandrium rubrum	subsp. *lapponicum* SIMM. (partly).
Myosotis silvatica	*M. alpestris* SCHMIDT (partly).
Solidago virgaurea	var. *alpestris* (W. et K.) DC.
Spiræa ulmaria	
Succisa pratensis	

It is not thought to be an exaggeration of facts when it is stated that the method employed here in systematising the various hereditary habitat types within the species is of great importance to both ecology and systematism. It is believed to be of distinct advantage when the nomenclature of ecologically corresponding forms is uniform and when the nature of the various forms can be deduced from the name. We are, however, as yet very far from being able to systematise any single species-population in the way here indicated, and much work, including the study of numerous cultivated series from differents points within the area of distribution of the different species, has to be done before this can be attempted. It must be emphasised, however, that investigations in the ecology and the geographical distribution of organisms, which aim at a serious attack on the problems, necessarily involve the study of the species along the lines here outlined.

The grouping of the species populations into ecotypes also signifies an endeavour to found a natural system of life-forms, a much debated problem in ecological literature. It is an attempt to overcome the difficulties felt by the investigators in this field and duly formulated by RAUNKIÆR (1914, p. 201) in the following way: »As we at least at present have no means of finding out how to see the unity in life-form in species of very different habitus and morphology (in the broadest sense of the word) we are compelled for the present to conclude that plants of different morphology belong to different life-forms, as long as these differences are thought to express adaptation to the environment.» With the increase in our knowledge of ecotypes, now in its beginning, a natural system of life-forms will doubtlessly be built up. There can be no doubt as to the great importance of such a system for the understanding of the interrelations of plants and habitats, as well as for the natural classifition of plant communities, in spite of the opposite views of some writers as regards the latter question.

III. GENOTYPICAL CONSTITUTION AND GEOGRAPHICAL DISTRIBUTION.

There is an old saying in plant-geography which states that a species occurs most abundantly at its centre of distribution, or as COWLES (1901) puts it a species »in general can grow in the largest number of formations at its centre of distribution, since there the

climatic conditions favour it most highly. In other regions, especially near its areal limits, it can grow only in those formations which resemble most closely in an edaphic way the climatic features at the distribution centre». Translated into modern genecological language the statement implies that in certain regions the climate favours the differentiation of the greatest number possible of various biotypes, which then become secondarily clustered in ecotypes to fit the various habitats, or »ecological niches», of the region. The behaviour of *Hieracium umbellatum* in Scandinavia (see TURESSON 1922) seems to be a good illustration of such a case. It was there shown that the different forms of the species found in different habitats were hereditary in nature and not habitat modifications. Is was also pointed out that the differentiation of the various ecotypes of that species had in all likelihood taken place separately at different points within the distribution area. Other facts were also given to show that the old belief in the great power of plants to populate various habitats in nature by means of modifications did not hold true, the course followed being a genotypical differentiation of the species-population into hereditary habitat types.

We are thus forced to consider the genotypical constitution of the species-population at different points within the area of distribution as a question of primary importance. No matter how »favourable» the climate may be in a certain diversified region — if the genotypical constitution is such as to prevent the differentiation of various habitat types to suit the different habitats — the plant then becomes rare within that region. In the further consideration of this question the behaviour of the alpine types differentiated in the Alp range and in Scandinavia will be discussed. We shall commence with oect. *alpinus* of *Melandrium rubrum, Ranunculus acer, Rumex acetosa* and *Geum rivale.* The study of this group of species has disclosed the remarkable fact that, while found in the lower regions of the Alps, they do not here enter *regio alpina* unless in particularly sheltered places. While in Scandinavia a specialised alpine type, oect. *alpinus,* is found in all four species, no such type has become differentiated in the Alp range, with the possible exception of *Geum rivale.* The most probable explanation of this fact is that the populations of these species in the Alp range have such a genotypical composition that an oect. *alpinus* cannot become realised. It might be argued that the environmental conditions of *regio alpina* in the Alps and in Scandinavia are not comparable, the conditions of light and

humidity, for instance, being different. However, we should then expect the alpine types of the two regions to be somewhat different from one another, as is probably the case with regard to the alpine types of *Solidago virgaurea* and the subalpine types of *Myosotis silvatica,* but we should hardly expect them to be completely absent in one of the regions. The view here held as to the cause of the lack of alpine types of these species in the Alps is considerably strengthened when it is seen that even in Scandinavia the alpine types may be absent in certain regions, in spite of the fact that the species are found in *regio subalpina* but not in *regio alpina* proper. According to my own findings the alpine types of *Rumex acetosa* and *Geum rivale,* for instance, are altogether lacking in the central Scandinavian mountain district, a fact corroborated by the vegetational studies within this region made by SMITH (1920). The differentiation of the alpine ecotypes of these species would most likely have taken place in this region if the genotypical composition of the species-populations allowed the realisation of such types.

The differences in the genotypical composition of a species-population in the north and south, or in the west and east, of its area of distribution is readily explained when seen from a genecologic point of view. In distributing itself over an area comprising different climatic belts the species-population becomes simultaneously zoned into climatic types, which we have called climatic ecotypes. The ecotype found of *Solidago virgaurea* in southern Germany is thus different from the ecotype of the same species in southern Sweden, and the ecotype of *Melandrium rubrum* with thin and delicate leaves, commonly found in Middle Europe, is only found in the southern part of Sweden (probably only in the beech woods of Scania). The ecotypes of the intermediate zones are naturally more like each other and therefore have generally remained unnamed, while the types at the extreme northern and southern points of the area of distribution often show marked differences from each other and therefore have aroused the interest of the systematists (cf. *Alnus incana β borealis, Prunus padus β borealis, Pinus silvestris β lapponica,* etc. of our floristic handbooks). However, the point to be specially emphasised in this successive change of the species with the different zones is the successive loss of genotype factors which undoubtedly results. The sorting and controlling effect of the environmental factors upon the species-population involves an elimination of those combinations which are unable to support life in a given zone. The elimination of certain combina-

tions also means a dropping out of certain factors, and the successive genotypical responses to different climatic zones thus result in a successive factor-depauperation of the species-population. The failure on the part of a certain ecotype, say oect. *alpinus,* to reappear when the habitat reappears is thus caused by the dropping out of the oect. *alpinus*-determining factors on the way to the alpine region of the Alp range. If this be so we should certainly expect to find the converse case, viz. species with alpine types differentiated only in the Alp range and not found in Scandinavia. This also happens to be true. There is a distinct group of species (including *Scabiosa columbaria, Silene venosa, Trifolium pratense),* which, although distributed in Scandinavia, has no alpine types differentiated except in the Alp range (*S. columbaria lucida, S. venosa alpina, T. pratense nivale,* now all included in my cultivated material). Differences in the genotypical composition of the species-population in the north and the south may also explain the two subalpine types in Scandinavia and in the Alp range of *Campanula rotundifolia,* the differences of which are too marked to be due only to differences in the climate of the two regions.

The time of the differentiation of oect. *alpinus* of the first mentioned species group is at this stage of our knowledge a matter of pure speculation. It is of great significance, however, that subfossil findings of some of these plants from interglacial time have been made (*Melandrium rubrum* in REID 1911, *Ranunculus acer* in WEBER 1915). These plants have thus been flourishing upon the ice-free tundras of Middle Europe, which remained unglaciated during the last epoch of glaciation. Then again it appears probable that it was just alpine ecotypes of these species that endured life on this tundra, at least at the maximum glaciation. That these types followed the northern border of the retreating ice sheet and not at the same time the southern border into the Alps may be explained by climatical differences in north and south, which must have become established soon after the initial melting of the ice, causing an early zonation of the vegetation in the way contemplated by WEBER (1915, p. 45).

Facts may also be deduced which favour the idea that part of these highly alpine ecotypes became locked up in the ice-free localities in Norway during the last epoch of glaciation (cf. FRIES 1913). However this may be, and no matter in what geologic period, the differentiation and the zonation of the species-population in climatic ecotypes are most important facts for plant-geography. The successive loss of genotype factors which undoubtedly results with the

spread of a species from north to south or from east to west is another important question, which has to be seriously considered when the ways and methods of plant migration are being discussed.

If LYELL's principle of uniformity in the action of forces in the present and past be accepted, the significance of the loss of genotype factors with the horizontal spread of a species over the earth's surface becomes of still greater moment when projected »vertically» through geologic time. According to the theory of combination (cf. TURESSON 1922, p. 343) we should expect that the reappearance of a certain geological period, say, at the appearance of each of the many periods of glaciation now known to geologists, would bring about the reappearance of identical organic forms. However, the elimination of certain forms and the subsequent loss of genotype factors during intervening periods make this reappearance impossible. Therefore »evolution» becomes of necessity successive and directive.

IV. GENECOLOGY AND THE SPECIES QUESTION.

Since the appearance of my first paper (TURESSON 1922 a) there have been published two works which aim at an ecological attack on the species question. (CLAUSEN 1922 and HALL and CLEMENTS 1923). The work of HALL and CLEMENTS, which on account of its careful analysis of critical plant genera no doubt marks a new epoch in North American taxonomy, is prefaced by an introduction in which questions of nomenclature, of species concept and of »methods and results in evolutionary taxonomy» are discussed. It is much to be regretted, however, that the authors do not make use of current and recognised terms in genetics, e. g. modification and hereditary variation, phenotype and genotype, etc. In the absence of a strict genetical terminology the understanding of the views propounded by the two writers becomes hardly possible. When my work (TURESSON 1922) is cited in connection with the following statement: »When plants are not plastic, however, extreme conditions furnish the only method of breaking the structural habit and thus permitting adaptation» (l. c. p. 22) nobody knows whether »adaptation» is meant to stand for habitat modification or whether it means selection within existing biotypes, and the word »plastic» because of its plasticity does not facilitate the understanding of the sentence. If, however, »adaptation» is here meant to imply the development of habitat modifications the generalisation made cannot be supported by my work. Although a

few instances of merely habitat modifications have been noted during my work the overwhelming number of hereditary habitat types — it is true, often secondarily masked by the modificatory effects of the habitat factors — indicate quite another course in the development of »adaptations». In reply to the reference to my work made by HAUCH (1924) with regard to the occurrence of different growth forms of *Fagus silvatica,* I am also much inclined to think that hereditary differences are of the much greater importance.

In an interesting paper on *Viola tricolor,* CLAUSEN (1922) finds a close parallelism between my ecotypes of *Hieracium* and *Atriplex* and the West-Jutland types of *Viola tricolor.* In a further discussion the species question receives due attention. He also points to the necessity of the maintenance of the binomial for the Linnean species as including all its minor units, which latter by means of trinomial should be related to the proper specific stock. The minor units to be distinguished are microspecies and isoreagents (the latter unit advanced by RAUNKIÆR 1918 b; JOHANNSEN'S older term isophene covers the same thing and ought therefore to be used, as already pointed out by KRISTOFFERSON 1923).

Progress in the species question and systematism is ensured along quite other lines, according to my own findings (TURESSON 1922, 1922 a, 1923). The ecological concept of the species there advanced makes a natural grouping of the Linnean species or *ecospecies* in my own terminology possible, as well as of the sub-units of the ecospecies, the *ecotypes.* Moreover, the habitat modifications of the ecotypes, the *ecophenes* in my terminology, of which instances have been given in the present paper, although not yet systematically treated, show us in which way the ecotypes may become modified through environmental conditions. The study of the species along these lines will also enable us to reach uniformity in nomenclature, as instanced by the treatment of certain ecotype groups in the present work. It is true, the ways and methods of such a line of research are necessarily different from those hitherto followed in systematism. The object of systematism, however, is or should be the distinguishing of units serviceable in other departments of biology. It cannot then be a matter of indifference, to ecology or to plant-geography, for instance, whether the prostrate »isoreagent», say of *Atriplex litorale* (TURESSON 1922), is a habitat modification or a hereditary habitat type, nor can it be immaterial whether the

»microspecies» *Viola tricolor maritima* SCHWEIGG. is a chance isolation or an ecotype.

I shall not here enter further upon the details of a suitable and natural nomenclative system the outline of which must be postponed to another occasion.

The inability of looking at the species problem from an ecologic point of view is also reflected in the treatment of the species problem by DU RIETZ (1923), who argues that the apogamic clones in *Hieracium, Taraxacum,* etc. are to be treated in the same way as the Linnean species and be named binominally as these: »eine Art ist eine Art, ganz gleichgültig ob sie *Diapensia lapponica, Viola tricolor* oder *Hieracium marginelliceps* heisst» (l. c. p. 241; cf. also SAMUELSSON 1922, p. 227). Instead of considering the advantages of distinguishing different kinds of species the species concept is made narrow or wide according to demands. The test is whether the units are »natürlich abgegrenzt», and whether the »Lokalrassen», as DU RIETZ puts it, are sufficiently different from the »Normaltypus» (l. c. p. 249). Apart from the untenability of the view of a given »Normaltypus» within a species-population the delimitation of the units according to the magnitude of the differences does not mark any improvement of the arbitrary methods hitherto used in the species making of so many systematists.

The risky consequences of such a species concept is also seen in the ideas of evolution developed by DU RIETZ. On account of the fact that in the migration of a species-population sometime only part of the biotype mass may be involved the statement is made that certain vital biotypes present in the original distribution area cannot become realised in the new area, as they did not happen to be among the migrants, their places being taken by other biotypes, which in the original area were less vital, and — »eine neue Art ist entstanden» (l. c. p. 251). Inevitably the question arises: what kind of a species? According to the author apogamic clones, Linnean species and, if I am right, certain ecotypes are all to be classed as species. The evolutionary history, however, of these three kinds of units is doubtless so different that a closer specification would not seem out of place.

The difficulties already existing for a profitable discussion of the species question and related problems are considerably increased by the arbitrary use of established, genetical terms practiced in the writings of DU RIETZ and others upon these questions. When the ideal systematist is said (DU RIETZ 1923, p. 236, see also DU RIETZ

1921, p. 12) to be endowed with a power of abstracting so much from the phenotype that he is able to see the genotype then this no doubt testifies to an enviable sharpsightedness not found among professional geneticists. The question may be raised, however, whether this optimistic view as to the cleverness of the systematist may not be due to ignorance on the part of the writer in the usage of the terms phenotype and genotype.

SUMMARY.

1. Cultivated material of a number of species has disclosed the differentiation of ecotypes in the following species: *Artemisia campestris, Rumex acetosella, Silene maritima, Allium Schoenoprasum, Lythrum salicaria, Plantago major, Spiræa ulmaria, Succisa pratensis, Myosotis silvatica, Geum rivale, Leontodon autumnalis, Ranunculus acer, Melandrium rubrum, Rumex acetosa, Campanula rotundifolia,* and *Solidago virgaurea.*

2. Ecotypes specialised to the calcareous rock formation (»Alfvar») on Öland have been found in *Artemisia campestris, Rumex acetosella, Silene maritima, Allium Schoenoprasum* and *Leontodon autumnalis.* Subalpine ecotypes have been found differentiated in *Spiræa ulmaria, Succisa pratensis, Myosotis silvatica, Geum rivale, Melandrium rubrum, Campanula rotundifolia,* and *Solidago virgaurea.* Alpine ecotypes have been found differentiated in *Myosotis silvatica, Geum rivale, Leontodon autumnalis, Ranunculus acer, Melandrium rubrum, Rumex acetosa,* and *Solidago virgaurea.*

3. It is pointed out that in certain cases the habitat modifications of these ecotypes have been named by systematists, the diagnoses of which therefore rest on modificatory characters. In a cultivated state these plants therefore do not any longer match the diagnoses given. It is also pointed out that named forms exist, which probably in one author are merely modifications, in others hereditary variations.

4. It is shown that a differentiation of parallel ecotypes takes place within different species, and the significance of this fact for systematism is pointed out. This parallel differentiation makes a uniform naming possible, which does away with the great mass of varietal names given to the different forms.

5. The following ecotypic names are proposed: oecotypus *campestris*, oect. *arenarius*, oect. *salinus*, oect. *subalpinus*, oect. *alpinus*, and the ecotypes of the different species investigated are placed in their respective groups.

6. The zonation of the species-population in climatic ecotypes is discussed in connection with the geographical distribution of oect. *alpinus* in different species. Species are mentioned which have oect. *alpinus* differentiated only in the Scandinavian mountains but not in the Alp range, and vice versa. The loss of genotype factors with the elimination of certain biotypes from a species-population, which distributes itself over an area comprising different climatic belts, makes this peculiarity intelligible.

7. It is pointed out that this factor-depauperation, which undoubtedly results as a consequence of the horizontal spread of a species-population through different climatic zones, becomes of still greater moment when projected »vertically» through geologic times. Because of the loss of genotype factors during intervening periods the reappearance of a certain geologic period cannot cause the reappearance of identical organic forms. Therefore »evolution» is of necessity successive and directive.

8. The relation of genecology to the species question is shown in a discussion of the various ideas expressed by other writers in the field of systematism and related lines of research.

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DIE REZIPROKEN BASTARDE ZWISCHEN GERANIUM BOHEMICUM L. UND SEINER UNTERART *DEPREHENSUM ERIK ALMQ.

VON *K. V. OSSIAN DAHLGREN*
UPPSALA

(With a summary in English)

I. VERBREITUNG VON UND FRÜHERE VERSUCHE MIT GERANIUM *DEPREHENSUM.

DIE interessante Unterart von *Geranium bohemicum* [1], welche *deprehensum* [2] genannt wird, zeichnet sich durch eine ganze Reihe konstanter Merkmale aus, die sie gegen die Hauptart scharf abgrenzen. Im Gegensatz zu dieser haben die *deprehensum*-Exemplare kleinere und anders gefärbte Samen (DAHLGREN 1923, Fig. 1), Keimblätter ohne Einschnitt, Laubblätter von abweichendem Typus, kleinere Blüten und rote Narben (Fig. 1, 2 und 9).

Die Pflanze wurde zum ersten Mal im Jahre 1910 in einem einzigen Exemplar zusammen mit der Hauptart in der schwedischen Provinz Småland bei Ekvik unweit der Stadt Västervik gefunden. Laut Angabe des Autors der Unterart, ERIK ALMQUIST (1916, S. 413), ist sie vom Entdecker, Professor Dr. ERNST ALMQUIST, im Herbst 1916 in noch einem Exemplar beobachtet worden, nämlich beim Kötnergut Draget, einen Kilometer südlich vom genannten Fundort; weiter auf einem neuangelegten Strasssendamm bei Saltsjöbaden unweit Stockholm, wo die Pflanze in etwa zehn Individuen zusammen mit der Hauptform vorkam. Professor ALMQUIST hat mir schliesslich gütigst mitgeteilt, dass er die Pflanze seitdem in Hunderten von Exemplaren an ganz verschiedenen Orten um Saltsjöbaden herum während mehrerer Jahre beobachtet hat. Auch bei Dalarö ist sie gefunden

[1] Einer meiner Schüler, G. RÖRBY, hat mir mitgeteilt, dass er 1923 in der Provinz Uppland, Kirchspiel Gottröra, unweit des Hofes Frubord eine Brandstätte mit lauter *weissblühenden* Exemplaren gefunden hat.

[2] E. ALMQUIST schreibt allerdings konsequent »*depraehensum*», was natürlich fehlerhaft ist. Ich glaube aber nicht allzu sehr gegen die Nomenklaturregeln zu sündigen, wenn ich ohne weiteres die richtige Buchstabierung einführe.

worden. In der Umgebung des Originalstandortes hat man sie in einer Weide an Stellen, wo Haufen von Reisig verbrannt worden waren, wiedergefunden.

Fig. 1. Links oben Blattrosette von *Geranium bohemicum;* links unten von *Geranium *deprehensum;* rechts *G. *deprehensum* × *bohemicum.*

Samen aus Saltsjöbaden und den Standorten in Småland sind mir gütigst zur Verfügung gestellt worden, und ich habe den *deprehensum*-Typus in jeder Hinsicht konstant gefunden. ERIK ALMQUIST

bemerkt allerdings (1916, S. 414) nebenbei, dass bei Saltsjöbaden Zwischenformen vorzukommen scheinen. Das ist sicher fehlerhaft. Das Auftreten des *deprehensum*-Typus an mehreren von einander weit getrennten Gebieten, seine sterilen Bastarde mit *G. bohemicum* und seine Dominanz gegenüber der Hauptart — die Keimblattform ausgenommen —, dies alles spricht bestimmt dafür, dass wir es nicht — wie ich zuerst annahm — mit einer unbedeutenden Varietät der Hauptart zu tun haben, sondern mit einer Form von bedeutend höherem systematischem Wert.

In der Festschrift für NILSSON-EHLE habe ich (1923) über die merkwürdigen Resultate der Kreuzung *Geranium bohemicum* × *deprehensum* berichtet. Die Bastardkeimblätter waren alle weiss (gelbweiss) und grün marmoriert. Die weisslichen Partien überwogen. Die folgende Entwicklung hat sich verschieden gestaltet, je nachdem der Vegetationskegel innerhalb eines mehr oder weniger grünen oder eines ganz chlorophyllosen Gebietes lag. Im letzten Falle, der am häufigsten vorkam, starben die Pflanzen bald an Kohlenhydrathunger; waren dagegen im Vegetationskegel normale Chloroplasten neben den anormalen vorhanden konnte eine Aufspaltung in grüne und weisse Partien stattfinden. Das Ergebnis konnte ein kräftiges, reichblühendes Individuum mit überwiegend rein grünen aber auch mit einigen chlorophyllosen Partien sein.

Fig. 2. Oben *Geranium bohemicum*; in der Mitte *G. *deprehensum*; unten links *G. bohemicum* × **deprehensum*, rechts *G. *deprehensum* × *bohemicum*.

Die Übereinstimmung mit dem allbekannten Versuche BAURS (1909) mit *Pelargonium* war ja auffallend. Er hat normalgrüne Exemplare mit weissen oder solchen mit Weissrandblättern gekreuzt und buntblättriges Abkommen erhalten. Die Erklärung dazu ist nach BAUR in dem Umstand zu suchen, dass die befruchtete Eizelle sowohl

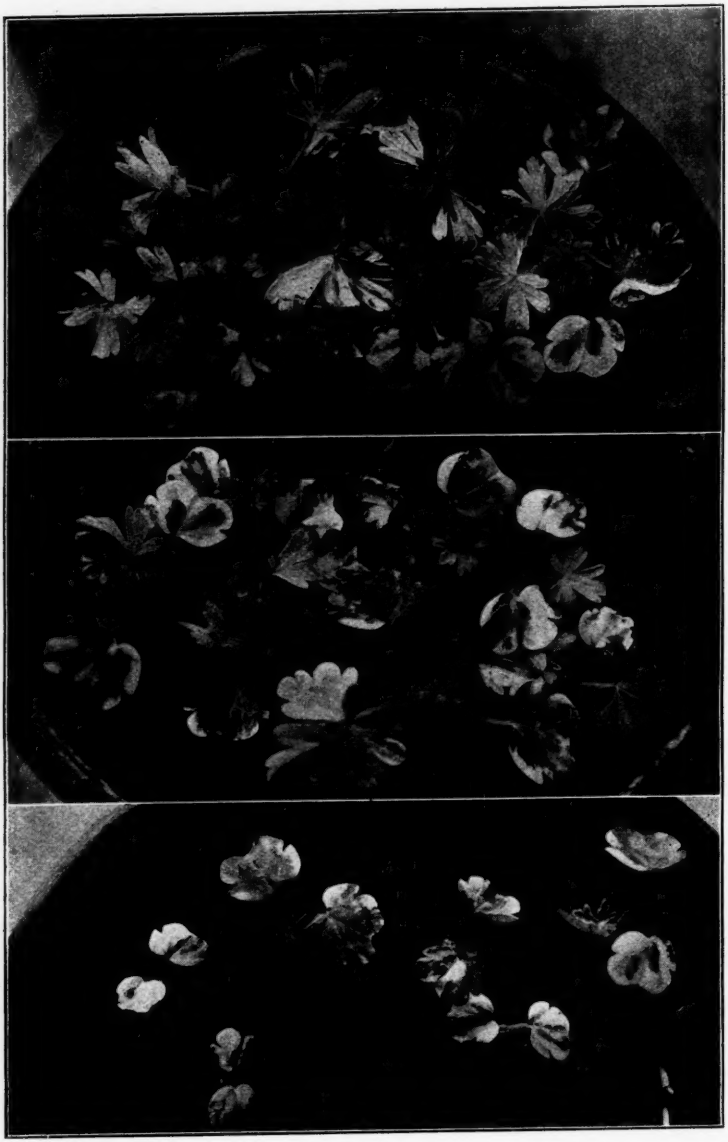

Fig. 3—5. Drei successive Stadien ($^{13}/_5$, $^{20}/_5$ u. $^{28}/_5$ 1924 photo.) der Entwicklung von *Geranium bohemicum* × **deprehensum* (aus Saltsjöbaden). Fig. 5 etwas verkleinert.

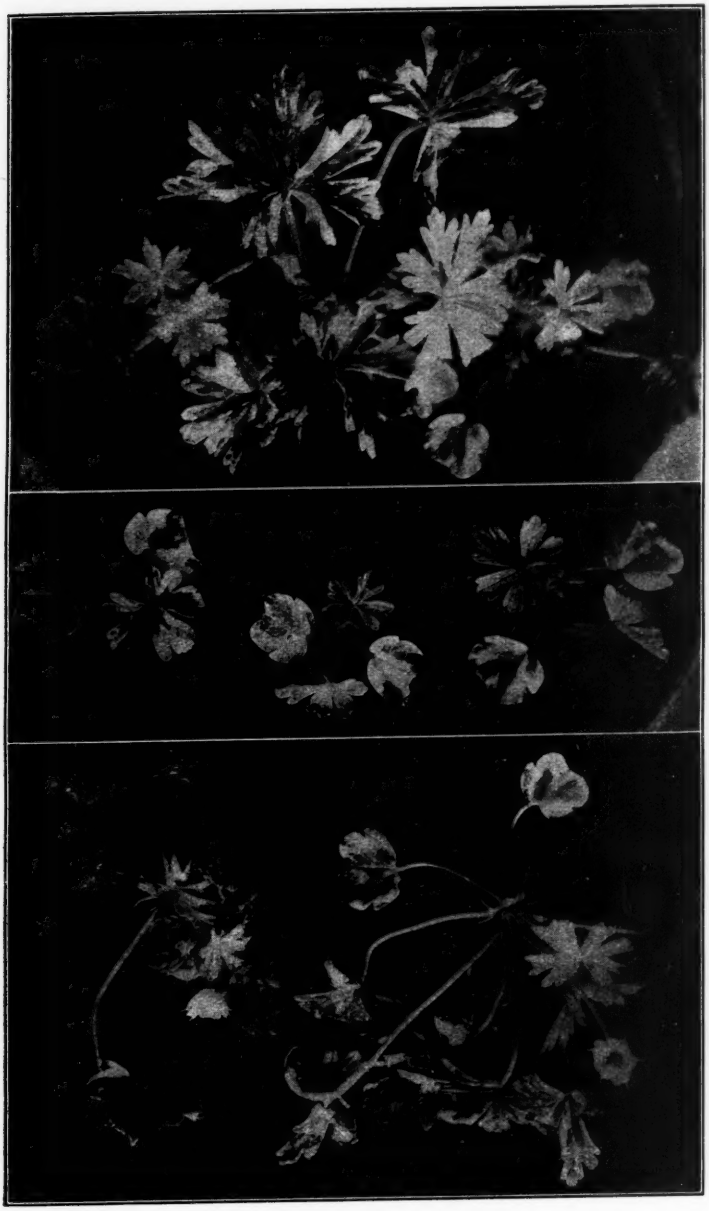

Fig. 6—8. — Fig. 6. Zwei Pflänzchen aus denjenigen in Fig. 5, $^{7}/_{7}$ 1924 photo. Nat. Gr. — Fig. 7—8. *Geranium bohemicum* × **deprehensum*, zwei Stadien, $^{30}/_{5}$ und $^{30}/_{6}$ 1924 photo. Die mittlere Pflanze hat später ein paar Blüten erzeugt. Fig. 8 etwas verkleinert.

normale als auch nicht ergrünungsfähige Plastiden enthält. Bei den Teilungen der Eizelle verteilen sich diese auf die neuen Zellen und dabei kann es vorkommen, dass Zellen entstehen, welche entweder lauter normale oder lauter untaugliche Chromatophoren enthalten. Die Descendenten der erstgenannten bestehen natürlich aus nur grünen Zellen; von den letztgenannten rühren die chlorophyllosen Gewebepartien her.

In BAURS Versuchen war die eine der Elternpflanzen (oder wenigstens derjenige Teil der Pflanze, welcher Geschlechtszellen bildet) chlorophyllos. Bei *Geranium* waren beide Eltern grün. Um meine gescheckten Pflanzen durch die Kreuzung *bohemicum* × *deprehensum* zu erklären, nahm ich folgendes an: In den Bastardzellen seien wohl die durch Pollenschläuche eingeführten *deprehensum*-Plastiden einer normalen Entwicklung fähig, die in der befruchteten Eizelle befindlichen *bohemicum*-Plastiden dagegen nicht. Die Scheckigkeit der Bastarde sollte — wie BAUR für *Pelargonium* angenommen hat — auf einer allmählich verlaufenden Entmischung der beiden Chromatophorensorten beruhen. Da die weissen Partien bei den Keimpflanzen in der Regel bedeutend überwogen, nahm ich an, dass es eben das Grüne war das von *deprehensum*-Plastiden herrührte, welche wohl verhältnismässig sparsam zusammen mit dem Spermakern in die Eizelle hineingelangen konnten. Die weissen Partien dagegen sollten aus den in der Eizelle vorhandenen zahlreichen *bohemicum*-Plastiden stammen. Diese meine Arbeitshypothese war natürlich leicht zu prüfen, wenn man die Bastarde in entgegengesetzter Weise herstellte, d. h. *G. deprehensum* × *bohemicum*. Samen dieser Kombination, die ich schon früher hatte, keimten leider nicht. Nun ist es mir jedoch gelungen, solche Bastardpflanzen zu erhalten; siehe hierüber weiter unten.

II. GERANIUM BOHEMICUM MIT DEPREHENSUM-EXEMPLAREN AUS SALTSJÖBADEN GEKREUZT.

Es interessierte mich zu sehen, ob *G. bohemicum* mit *deprehensum*-Exemplaren[1] aus Saltsjöbaden gekreuzt ähnlich reagierte wie

[1] Die Samen wurden in der früher beschriebenen Weise (DAHLGREN 1923, S. 243) behandelt; doch habe ich die Samenschale nach der Wärmebehandlung oft vorsichtig geschabt. In diesem Zusammenhang ist es vielleicht von einigem Interesse auf ein paar Untersuchungen von GAIN (1922, S. 1031 und 1557; 1924, S. 865) aufmerksam zu machen. Er hat einige Samen von *Helianthus annuus*

bei Kreuzung mit Individuen vom Originalstandort. Dies war auch der Fall. Fig. 3—6 zeigen vier suczessive Altersstadien einiger Bastardpflanzen, und in Fig. 7—8 sind zwei andere dargestellt. Wie man sieht, sind sie stark gescheckt, und während der Entwicklung findet eine vegetative Aufspaltung statt. Zwei von jenen Pflanzen entwickelten sich zu blühenden Zwergindividuen (Fig. 6), trotzdem die Hauptachse aus nur chlorophyllosen Teilen bestand. Nach einer anderen Kreuzung erhielt ich ausser einigen bald abgestorbenen Pflänzchen zwei ganz kräftige. Bei diesen erschienen die marmorierten Teile bald immer seltner, und schliesslich bildeten sich nur rein grüne, eine kleine Anzahl weisse sowie einige periklinal geteilte Sprösse aus. So konnte man z. B. einen weissen Streifen am Stengel verfolgen, von dem ein weisses Blatt herrührte, während das entgegengesetzte Blatt ganz grün war. Eine Sache verdient hier hervorgehoben zu werden. Nachdem ich Mitte September ein altes Exemplar in mein Schreibzimmer gestellt hatte, wo es einen ziemlich schattigen Platz erhielt, beobachtete ich, dass die weissen Blätter nach und nach eine grüngelbe Färbung annahmen. Es scheint demnach so zu sein, dass die — vermuteten — *bohemicum*-Chromatophoren bei schwacher Beleuchtung Chlorophyll entwickeln können. Die Beobachtungen wurden leider nur an einem einzigen Exemplar gemacht, aber für die Richtigkeit der Erklärung spricht der Umstand, dass bei Keimpflanzen, welche in der Sonne wachsen, die chlorophyllosen Partien reiner weiss sind als bei solchen, welche im Zimmer aufgezogen wurden; bei diesen haben die betreffenden Partien einen Stich ins Gelbliche. ÅKERMAN (1922) hat eine *lutescens*-Sippe von Hafer beschrieben, welche im direkten Sonnenlichte nicht lebensfähig war, sondern auf freiem Felde binnen kurzer Zeit vergilbte.

sogar bis auf 150° C erhitzt und andere während einer halben Stunde einer Wärmebehandlung von 130° ausgesetzt und trotzdem Keimung erhalten.

Wie ich vorher gezeigt habe (DAHLGREN 1923, S. 241) können Samen von *G. bohemicum* während sehr langer Zeit, mindestens 60 Jahre, ihre Keimfähigkeit behalten, wahrscheinlich aber während mehr als eines Jahrhunderts. Hierfür spricht ja entschieden das plötzliche Auftreten der Pflanze an Brandstätten in einem alten Wald. OHGA (1923, S. 87) hat neulich einen interessanten Fall von lange beibehaltener Keimfähigkeit bei *Nelumbo nucifera*, welche in der Erde geruht hat, mitgeteilt. In den Ablagerungen eines schon längst entwässerten Sees in der südlichen Mandschurei hat man taugliche Samen dieser Pflanze angetroffen. Das Alter der dort wachsenden Bäume wurde auf mindestens 130 Jahre geschätzt, »although it is probable that the seeds have remained buried 200 years or even 400 years». Über lange beibehaltene Keimfähigkeit siehe z. B. MOLISCH (1918, S. 288) und SHENSTONE (1923, S. 297) und dort zitierte Literatur.

Neulich hat auch NOACK (1924, S. 80) bei *Pelargonium zonale* Sprösse mit sonst reinweissen Blättern beobachtet, bei denen die Ser-

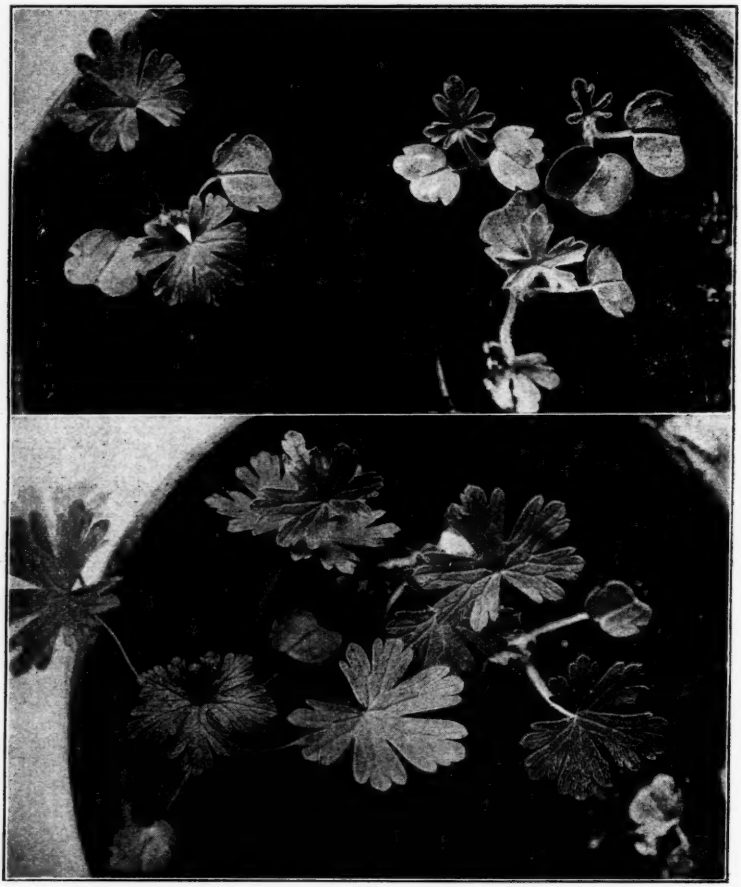

Fig. 9—10. *Geranium *deprehensum* × *bohemicum*, $^{20}/_{5}$ und $^{28}/_{5}$ 1924 photo. Man beachte die ganz winzige Panachüre der Keimblätter; Laubblätter ohne jede Spur davon. In Fig. 9 rechts oben eine Keimpflanze von *G. *deprehensum*, durch Selbstbefruchtung entstanden. Obs. Keimblätter ohne Einschnitt. Fig. 10 etwas verkleinert.

raturspitzen diffus grün gefärbt waren, sobald die Pflanzen unter ungünstigen Temperatur- und Beleuchtungsverhältnissen standen. (Bei derselben Spezies hat auch SCHÜRHOFF [1924, S. 175] — damit

ältere Angaben von ZIMMERMANN bestätigend — gefunden, dass alle Schliesszellen der Weissrandblätter in geringer Menge Chlorophyll führen).

III. GERANIUM *DEPREHENSUM × BOHEMICUM.

Mit besonders grossem Interesse habe ich die Keimpflanzen der umgekehrten Kombination erwartet, d. h. *deprehensum* × *bohemicum*. Ganz einerlei ob ein *deprehensum*-Individuum vom Originalstandort oder aus Saltsjöbaden als Mutterpflanze verwendet wurde, das Resultat war dasselbe. Die jungen Keimlinge waren alle wenig gescheckt (Fig. 9, 11 und, etwas bunter, 13). Verschiedene unter ihnen konnten sogar bei schnellem Hinsehen einen ganz grünen Eindruck machen. Die Scheckigkeit war doch sowohl betreffs Muster als auch Intensität ziemlich wechselnd, genau wie es bei Keimpflanzen der reziproken Kreuzung der Fall war. Die ausgewachsenen Exemplare zeigen oft nicht die geringste Spur einer Scheckigkeit (Fig. 10). Fig. 15 ist der einzige Fall von etwa zwanzig Pflanzen, welche ich beobachtet habe, bei dem die Stammknospe schliesslich nur untaugliche Chromatophoren enthielt. Fig. 12 zeigt ein Exemplar, bei dem ein Sektor der Pflanze bunt ist. Die Blätter (Fig. 1) und Blüten (Fig. 2) dieser Bastarden gleichen vollkommen denen der Kombination *bohemicum* × *deprehensum*, welche vorher (DAHLGREN 1923) beschrieben worden sind, d. h. sie stimmen mit dem *deprehensum*-Typus völlig überein. Von den *bohemicum*-Merkmalen dominiert nur der Einschnitt in den Keimblättern. Die Antheren sind verkümmert, öffnen sich nicht und enthalten nur plasmaarme, eingeschrumpfte und untaugliche Pollenkörner. Ich habe weit mehr als 200 Blüten mit Pollen von den Elternpflanzen belegt aber — wie früher — ohne Erfolg. Der Bastard ist steril.

Fig. 11. *Geranium *deprehensum* × *bohemicum* ($^{26}/_{5}$ 1924 photo). Das erste Laubblatt stark gescheckt.

Wenn man das Aussehen der Bastarde nach den respektiven Kreuzungen vergleicht, so ist der Unterschied ganz besonders auffallend. *Geranium bohemicum* × *deprehensum* gibt, wie gesagt, eine stark gescheckte Abkommenschaft, welche meistens lange vor dem

Blühen abstirbt. Die Kombination *deprehensum* × *bohemicum* dagegen ergibt relativ sehr schwach panachierte Keimpflanzen, bei denen die herauswachsende Stammspitze nur ausnahmsweise chlorophyllos ist. Diese Umstände sprechen ja sehr für die Richtigkeit

Fig. 12. *Geranium* **deprehensum* × *bohemicum*. Dieselbe Pflanze wie in Fig. 11 ($^{26}/_{6}$ 1924 photo). Ein Sektor der Pflanze ist bunt. $^{2}/_{5}$ nat. Gr.

meiner vorher referierten Ansicht, dass nämlich nur *deprehensum*-Chromatophoren sich in Zellen mit Bastardkernen normal entwickeln können.

IV. ANDERE FÄLLE VON BUNTEM NACHKOMMEN NACH KREUZUNG REINGRÜNER ELTERN.

Schon DE VRIES hat, ohne die Sache näher zu analysieren, einige Fälle mitgeteilt, wo mehrere Individuen nach gewissen *Oenothera*-Kreuzungen blassgefärbt oder gescheckt wurden. RENNER (1924 b) hat eine grosse Anzahl systematisch angestellter Kreuzungen ausgeführt. Er hat diese interessanten Verhältnisse ermittelt und in seiner diesen Sommer erschienenen Arbeit ausführlich beschrieben. Einige kurze Notizen sind in zwei Vortragsreferaten erschienen (RENNER 1922 und 1924 a). Er erklärt seine Ergebnisse — wie ich meine *Geranium*-Versuche — durch die Annahme, dass Plastiden bei der Befruchtung übergeführt werden, und dass diese bei gewissen Kern-

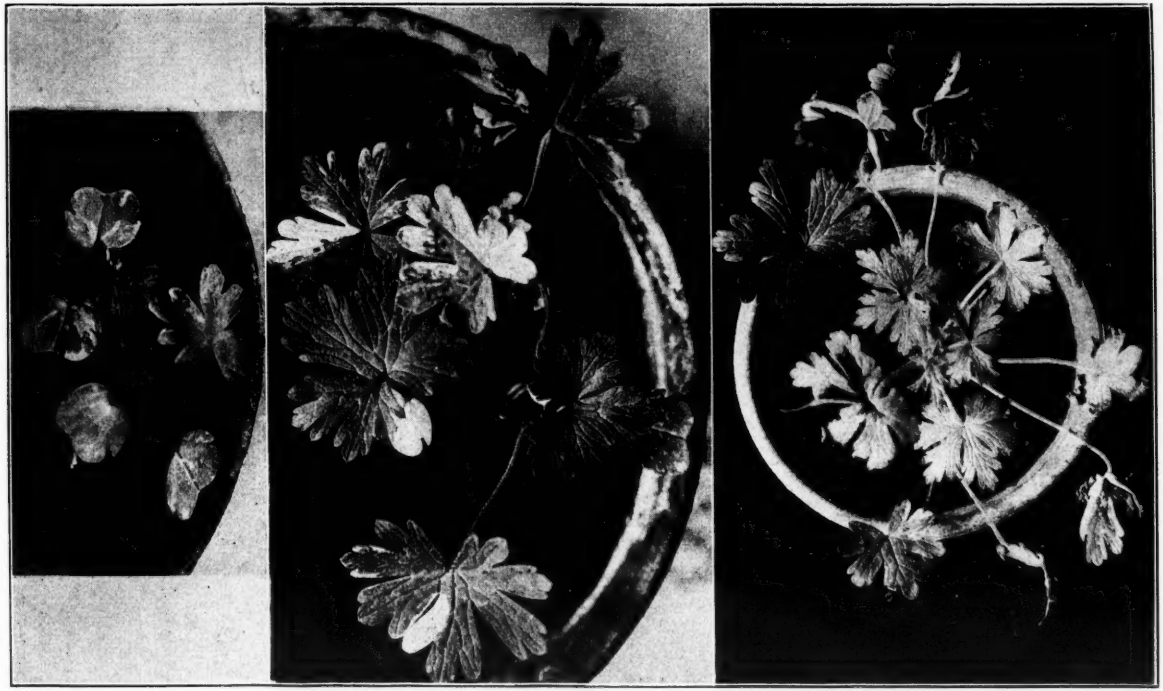

Fig. 13—15. *Geranium* **deprehensum* (aus Saltsjöbaden) × *bohemicum*. — Fig. 13. Die oberste Keimpflanze ist die, nach dieser Kombination der Elternpflanzen, am stärksten panachierte die ich gesehen habe ($^{20}/_{5}$ 1924 photo). — Fig. 14. Dieselben Pflänzchen $^{28}/_{5}$ photo. — Fig. 15. Das oberste Individuum $^{20}/_{6}$ photo., < $^{1}/_{2}$ nat. Gr. Die Sprossachse chlorophyllos, ein ungewöhnliches Verhältnis nach dieser Richtung der Bastardierung.

kombinationen nicht normalgrün werden können. Die Buntheit sollte auf einer vegetativen Aufspaltung, einer Entmischung der beiden Arten von Chromatophoren beruhen.

Ein Beispiel unter den vielen mag die Sache verdeutlichen. *Oenothera Lamarckiana* ist was RENNER einen Komplexheterozygot nennt, der die beiden Gametentypen »*gaudens*» und »*velans*» bildet. (Homozygotische Kombinationen sind nicht lebensfähig.) *Oenothera Hookeri* dagegen ist kein Komplexheterozygot, sondern alle ihre Keimzellen können als ^{h}*Hookeri* = *haplo-Hookeri* bezeichnet werden. Wenn bei der Kreuzung zwischen diesen Arten *Oenothera Hookeri* als Mutterpflanze verwendet wird, so werden beide Zwillingsbastarde, die sog. *laeta*- und *velutina*-Typen (= ^{h}*Hookeri* . *gaudens* und ^{h}*Hookeri* . *velans*), grün und kräftig. Bei der reziproken Kombination dagegen, *Lamarckiana* × *Hookeri,* werden auch die *laeta*-Individuen (*gaudens* . ^{h}*Hookeri*) normalgrün; aber bei den *velutina*-Pflanzen (*velans* . ^{h}*Hookeri*) werden schon »die Kotyledonen in der unteren Hälfte weisslich, und die Primärblätter der meisten Individuen sind von Anfang an ganz blass grünlichgelb oder weisslichgrün.» Derartige Individuen sterben sehr früh ab. Etwa 15 % der Keimpflanzen sind doch gescheckt mit normalgrün und spalten vegetativ in grüne und weisse Sprösse auf. Nach Selbstbefruchtung geben die Blüten an den grünen Sprössen rein grüne lebenskräftige Pflanzen und an den gelben eine rein gelbe, bald absterbende Abkommenschaft. RENNER ist nun der Ansicht, dass die sparsam auftretenden grünen Flecke auf eingeführten *Hookeri*-Chromatophoren beruhen, während die blassen dagegen von solchen von *Lamarckiana*-Ursprung herrühren; die letztgenannten können sich bei der Kernkombination *velans* . ^{h}*Hookeri* nicht normal entwickeln. Nur wenn eine genügende Menge *Hookeri*-Plastiden bei der Befruchtung hineinkommt, können die *velutina*-Pflanzen, welche sich aus der *Lamarckiana*-Eizelle entwickeln, sich am Leben erhalten. — Nimmt man *Hookeri* als Mutterpflanze, könnte man erwarten, dass einige Prozente der *velutina*-Pflanzen (^{h}*Hookeri* . *velans*) gleichfalls — wenn auch in weit geringerem Grade — scheckig werden sollten, genau wie bei dem Bastarde *Geranium deprehensum* × *bohemicum.* Sie werden aber in der Regel völlig normal. Nur ganz ausnahmsweise entsteht eine Pflanze mit gelben Flecken auf grünem Grund. RENNER (S. 311) ist der Ansicht, dass genannter Umstand darauf beruht, dass eventuell hineingelangte *Lamarckiana*-Plastiden sich in Zellen mit obenerwähnter Kernkombination sehr langsam vermehren, und dass also, da »die *Hookeri*-

Plastiden von vornherein in der Überzahl sind, selten Zellen entstehen werden, die nur *Lamarckiana*-Chloroplasten enthalten. Zweitens könnte der *Lamarckiana*-Pollenschlauch im allgemeinen weniger Leukoplasten ins Ei bringen als der der *Hookeri*.»

RENNER (l. c., S. 323) ist es u. a. auch gelungen zwei von verschiedenen Arten stammende Gen-Komplexe in das Plasma einer dritten Art zu bringen. »So wird *velans* von *Lamarckiana* durch die Kreuzung *biennis* × *Lamarckiana* ins *biennis*-Plasma gebracht, und zwar treten *velans*-Eizellen in den Verbindungen *albivelutina* = *albicans* . *velans* und *rubivelutina* (oder *fallax*) = *rubens* . *velans* auf. Werden diese beiden *velutinae* mit dem Pollen der *Oe. Hookeri* belegt, so sind die entstehenden Verbindungen *velans* . ^{h}*Hookeri* satt grün, ebenso wie mit *Hookeri*-Plasma, während mit *Lamarckiana*-Plasma die *Hookeri-velutina* ja sehr blass ist. Es zeigt sich also, dass die aus *Lamarckiana*- und *Hookeri*-Genomen zusammengesetzte Verbindung *Hookeri-velutina* mit dem Plasma einer dritten Art, *biennis*, besser zu ergrünen vermag als mit dem der einen Elternart, *Lamarckiana*.» Ein näheres Eingehen auf die vielen interessanten Versuche RENNERS kann natürlich nicht in Frage kommen. Sie lassen sich alle nach der Theorie erklären [1].

V. KRITISCHE BEMERKUNGEN ÜBER DIE THEORIE EINER ÜBERFÜHRUNG VON PLASTIDEN UND DEREN SPÄTERE ENTMISCHUNG ALS URSACHE DER PANACHÜRE.

Oft werden nur nackte Spermakerne in den Embryosack eingeführt. Dass aber bei verschiedenen Arten Sperma*zellen* mit dem Pollenschlauch hineingelangen können ist unzweifelhaft. In dieser Zeitschrift habe ich vorher einige derartige Fälle mitgeteilt und eine

[1] GATES (1923) hat neulich eine interessante Beobachtung bei F_2 und nachfolgenden Generationen nach der Kreuzung *Oenothera biennis* × *rubicalyx* mitgeteilt. Die Blütengrösse schwankt bei verschiedenen Individuen beträchtlich, gleich wie bei einer und derselben Pflanze; also auch eine somatische Spaltung. Um eine gewöhnliche Mendelspaltung handelt es sich nicht. Der Autor will die Unregelmässigkeiten wenigstens zum Teil, auf eine Vererbung durch das Zytoplasma zurückführen. Durch Einführung von fremdem Plasma sollte eine Störung in der harmonischen Entwicklung der Pflanzen eintreten. Wenn diese Auffassung richtig ist, wäre GATES' Untersuchung von ganz besonderem Interesse, da bisher alle anderen Fälle von zweifelloser Vererbung durch das Plasma sich auf die Panachüre beziehen. — In gewissen Fällen, wo die Abkömmlinge reziproker Verbindungen verschieden sind, dürften wir es wohl auch mit einer Wirkung von spezifischem Plasma der Eizelle zu tun haben.

photographische Aufnahme von *Plumbagella micrantha* reproduziert, wo man deutlich eine Spermazelle in Berührung mit dem primären Endospermkern sieht. (Siehe DAHLGREN 1921, S. 97 und Tafel III, wo die misslungene Fig. 6 im Lichtdruck wiedergegeben ist.) Einen besonders schönen Fall von Spermazellen in Berührung mit der Eizelle hat WYLIE (1923) bei *Vallisneria spiralis* konstatiert. Siehe übrigens TISCHLER (1922, S. 485). Es ist mir nicht gelungen Befruchtungsstadien in meinen Mikrotompräparaten von *G. bohemicum* zu erhalten.

RUHLAND und WETZEL (1924) haben neulich, besonders bei *Lupinus luteus,* Chloroplasten von minimaler Grösse in der generativen Zelle nachweisen können. Wenn also starke Gründe für die Annahme vorliegen, dass bei der Befruchtung zuweilen Plasma und Plastiden in die Eizelle eingeführt werden können, ist es natürlich aus leicht einzusehenden Ursachen kaum möglich die Sache auf rein zytologischem Wege einwandfrei zu beweisen [1].

In einer Arbeit über einige neue Fälle von *Albomaculatio,* d. h. Vererbung nur durch die Mutter, hat CORRENS (1922) einige theoretische Einwendungen gegen die Auffassung dieser Art Scheckigkeit, als auf einer Entmischung zweier Sorten Chromatophoren beruhend, gemacht. Wäre dies der Fall, würde man nämlich — vorausgesetzt dass sich die beiden Chromatophorensorten gleich schnell teilen — oft Zellen mit beiden Sorten vorfinden. Es lag damals doch nur eine einzige Angabe von GREGORY (1915, S. 309) vor, dass in jungen stark wachsenden Blättern einer albomaculaten *Primula sinensis* grosse grüne und kleinere gelbe Chromatophoren in derselben Zelle vorhanden wären. Sowohl CORRENS (l. c., S. 481) als NOACK (1924, S. 59 und 76), von denen der letzte neulich ähnliche Verhältnisse bei *Pelargonium zonale* gesehen hat, sind doch der Ansicht, dass wir es hier nur mit verschiedenen Entwicklungsstadien zu tun haben [2]. FUNAOKA (1924, S. 363) hat in diesem Jahre einige

[1] STOMPS (1920, S. 269; siehe auch 1917, S. 174) ironisiert darüber, »dass die Autoren, je nach den Bedürfnissen der von ihnen gegebenen Erklärungsweisen, die generativen Pollenschlauchkerne bald ohne Protoplasma, bald von Plasma und Chromatophoren begleitet in die Eizellen übertreten lassen». Die Übereinstimmung zwischen den Befruchtungsverhältnissen im Tier- und Pflanzenreich verpflichtet, meint er, »hier wenn irgendmöglich Übereinstimmung herrschen zu lassen». Dagegen kann man doch einwenden, dass sowohl nackte wie auch mit Eigenplasma umgebene Spermakerne im Embryosack beobachtet worden sind. Im letzteren Falle ist wohl ein Überführen von Plasma in das Ei wenigstens nicht undenkbar.

[2] Vgl. RANDOLPH (1922, S. 358); *Zea mays.*

von CORRENS' *albomaculata*-Pflanzen untersucht und dabei sowohl normale als auch farblose Chloroplasten in denselben Zellen gefunden. Über diejenigen bei *Stellaria media* lesen wir folgendes: »Sie enthält ausser einer geringen Zahl von normalen Chloroplasten noch farblose Plastiden. Diese Übergangsform ist dort reichlich vorhanden, wo weisse und grüne Zellen durcheinander liegen, und die Farbengrenze dadurch mehr oder weniger verschwommen aussieht.» Bei buntblättriger *Senecio vulgaris* waren auch derartige Zellen, jedoch spärlicher, vorhanden.

In einer albomaculata-Form von *Zea mays* (E. G. ANDERSSON, 1923) hat RANDOLPH (1922, S. 354) in derselben Zelle sowohl normale als farblose Chromatophoren nebst Übergangstypen zwischen diesen beobachtet. Von diesen Tatsachen aus schreibt er: »In the light of such facts the inapplicability of hypotheses involving a simple sorting out of plastids of two completely distinct types by successive cell divisions is clearly evident, so far as the color types in the strain of maize under consideration are concerned.»

Eine andere von CORRENS' Einwendungen bezieht sich auf die Zahlenverhältnisse, welche BAUR bei seinen bekannten *Pelargonium*-Versuchen erhielt. Nach der Kombination grün × weiss erhielt er nämlich nicht besonders viel mehr rein grüne Individuen (88 %) als nach der Kombination weiss × grün (73 %), trotzdem die Eizelle im letzten Falle ja lauter »kranke» Chromatophoren enthielt. Vielleicht beruht dies darauf, dass sich die farblosen Chromatophoren langsamer teilen als die grünen. NOACK (1924), der umfassende Versuche gerade mit *Pelargonium* ausgeführt hat, hat festgestellt, dass die Abkömmlinge im allgemeinen weit scheckiger werden, wenn die Mutterpflanze chlorophyllos ist, als wenn sie zu einer ganz grünen Sippe gehört[1]. Vom aller grössten Interesse ist seine Feststellung, dass verschiedene Individuen, sowohl grüne als albotunicatae, eine ganz verschieden starke Neigung haben bei Kreuzungen gescheckte bezw. farblose Keimlinge zu erzeugen. Den Ausdruck »stark» fügt NOACK solchen Pflanzen bei — mögen sie nun selbst grün sein oder Weissrandblätter haben —, welche ein stark buntes Nachkommen aufweisen. Er schreibt (l. c., S. 70): »Jeder dieser Pflanzen kommt eine ihr eigentümliche charakteristische Valenz zu, so dass die stärksten

[1] Dasselbe hat RENNER (l. c., S. 319) bei *Oenothera* gefunden und vielleicht auch BROŽEK (1923) bei einer albomaculata-Form von *Mimulus*, wenigstens wenn man nach einer Äusserung (S. 76) am Schlusse seiner Abhandlung urteilen darf.

Weissrand-Pflanzen mit den stärksten grünen gekreuzt in ihrer Nachkommenschaft den grössten Scheckungswert, die schwächsten Weissrandpflanzen mit den schwächsten grünen den geringsten Scheckungswert liefern.» Diese sehr interessante Beobachtung spricht ja gegen die Annahme, dass die wechselnde Stärke der Panachüre nur von dem Plastidenübertritt abhängig sein sollte.

Aus oben angeführten Gründen ist CORRENS der Ansicht, »dass es sich um eine Krankheit des *Plasmas,* nicht um eine der Plastiden handelt», eine Krankheit, die, wie in BAURS oben erwähntem Falle, eine gesunde Eizelle infizieren kann. Bis zu einem gewissen embryonalen Zustand des Gewebes besteht nach CORRENS in jeder Zelle der bunten Pflanze die Möglichkeit sich entweder normal zu entwickeln oder kranke Plastiden auszubilden. Ist der Charakter einer Zelle ein für allemal bestimmt, dann ist der Zustand dieser Zelle, oder ihrer Abkömmlinge, nicht umkehrbar. Das fertige Gewebe besteht also schliesslich, wenigstens für gewöhnlich, entweder aus nur kranken oder nur gesunden Zellen.

Wie aus dem oben angeführten hervorgeht, nimmt auch NOACK bestimmt von der Auffassung Abstand, dass die Buntheit von einer Entmischung grüner und nicht ergrünungsfähiger Plastiden abhängig sein sollte. Er behauptet doch, dass neben dem Plasma auch der Kern an dem Zustandekommen der Panachüre beteiligt sei. »Es handelt sich», meint er, »um einen indifferenten reversiblen Krankheitszustand beider Zellbestandteile, der im Laufe der Zellontogenie zu einem irreversibel kranken oder gesunden Zustand der einzelnen Gewebeelemente führt.» Er (1922, 1924) versucht auch mit aller Gewalt zu zeigen, dass bei *Pelargonium zonale* die ganze Blattmasse mit Ausnahme der Epidermis selbst sich aus einer einzigen subepidermalen Schicht des Sprossscheitels entwickelt. Bei BAURS Periklinalchimären dieser Pflanze müssen folglich die »Anlagen» sowohl für Grün als auch für Weiss in einer und derselben Zelle einmal vorhanden gewesen sein. Werden diese Resultate von NOACKS Untersuchungen wirklich bestätigt, dann wäre ja die Theorie, welche die Scheckigkeit als von dem Zusammenbringen verschiedenartiger Plastiden bei der Befruchtung und einer später einsetzenden Entmischung abhängig erklärt, totgeschlagen. Rätselhaft verbleibt in jedem Falle der Umstand, dass gerade die »Tunica» chlorophyllos ist, der »Kern» dagegen normal. Noch schwerer zu erklären werden auch die spontanen Chimären, bei denen die subepidermale Zellen-

schicht in ihren Kernen ein anderes Gen hat als die Zellen im Innern der Pflanze [1].

Die bunten Pflanzen, welche RENNER und Verfasser durch Kreuzung rein grüner Eltern erhalten haben und deren Grad von Buntheit, der je nach der Kreuzungsrichtung wechselt, werden von NOACK (1924, S. 82) als Störungen in den Stoffwechselsbeziehungen zwischen Kern und Plasma — die je nach der Kombination der verschiedenen Zellbestandteile verschieden ist — erklärt. »Selbstständige Plastidensorten und Plastidenübertritt bei der Befruchtung», schreibt er, »können auch hier zur Erklärung der Tatsachen nicht herangezogen werden».

SCHÜRHOFF (1924, z. B. S. 192—194), der dem Plasma und den Plastiden jede Spur von eigenem Einfluss auf die Erblichkeit der Panachüre abspricht, behauptet, dass diese ausschliesslich und immer vom Zellkern herrührt (also eine Art Verschärfung der Auffassung NOACKS). Er schreibt über unsere Versuche folgendes: »Durch die Kreuzung gewisser rein grüner Sippen kann im Diploidkern die Entwicklungstendenz für das Ergrünen der Chromatophoren rezessiv werden gegenüber dem Nichtergrünen. Wenn wir dabei im Auge behalten, dass eine solche Nichtergrünungstendenz normalerweise für die Epidermiszellen in den Diploidkernen lokalisiert ist, so haben wir es hier nur mit dem Dominantwerden einer im Kern bereits vorhandenen aber für das Assimilationsgewebe gewöhnlich rezessiv bleibenden Eigenschaft zu tun». Diese wenig durchgedachte Theorie übergehe ich mit Stillschweigen. Wie erklärt SCHÜRHOFF z. B. die verschiedene Scheckigkeit bei Abkömmlingen reziproker Kreuzungen?

Die Theorie, welche gewisse Arten von Scheckigkeit als mit Plastidenübertritt und späterer Entmischung zusammenhängend erklärt, ist ja durch ihre Einfachheit verlockend, braucht aber natürlich deswegen nicht richtig zu sein. Mehrere der Einwendungen, die CORRENS und besonders NOACK jetzt gemacht haben, sind sehr gut begründet. Um die Sache klarzulegen ist es von grösster Bedeutung,

[1] Einen in hohem Grade veränderlichen Erbfaktor hat jedoch CORRENS (1919) bei einer mendelnder sog. *albovariabilis*-Sippe von *Capsella bursa pastoris* nachgewiesen. Die Panachierung ist durch eine an ein Gen gebundene »Krankheit» bedingt, die ab- und zunehmen kann. Im völlig gesunden oder kranken Zustand ist der Status des Gens irreversibel. Er vermutet dass ähnliche Verhältnisse bei gewissen buntblättrigen Sippen von *Alliaria officinalis* und *Barbarea vulgaris* vorhanden sein können. Die wechselnde Scheckigkeit und die ziemlich schwankenden Zahlenverhältnisse, die ich (DAHLGREN 1921) und neulich Fräulein ANDERSSON (1924) bei der letzterwähnten Art gefunden haben, sprechen ja hierfür.

dass man, z. B. albomaculata-Formen, systematisch nach Zellen mit gemischten Plastiden sucht. Ehe dies in grösserem Masse als bisher ausgeführt worden ist, dürfte es vielleicht verfrüht sein das Problem definitiv lösen zu versuchen. Die Vererbungsweise der Panachüre ist bei verschiedenen Arten so ungleich, dass man sich bis auf weiteres wohl vorstellen kann, dass auch Vererbung durch Plastidenübertritt stattfinden könnte.

Uppsala, Botanisches Institut, Oktober 1924.

SUMMARY.

In a previous paper I have given a description of the new subspecies *Geranium bohemicum* **deprehensum*. The cross *G. bohemicum* × **deprehensum* resulted, as stated before, in green and white marmorated seedlings. I have repeated the cross with *deprehensum*-material from another place in Sweden and have got the same types of bastard plants (Fig. 3—8). Most of the seedlings are starved to death by insufficiency of chlorophyll. In general the green areas are comparatively small. I there suggested that this result would be understood by assuming the incapacity of the *bohemicum*-plastids to become green in cells with a bastard nucleus. The comparatively small green areas in the F_1-seedlings were suggested to be due to a transmission on a small scale of *deprehensum*-plastids into the egg during the fertilization process. A segregation of the two types of plastids may occur at cell divisions.

Our hypothesis is now tested by the reciprocal cross, *Geranium* **deprehensum* × *bohemicum*. In this case we get plenty of *deprehensum*-plastids — with the power of normal development in bastard cells — in the egg, and only a limited transport of inactive *bohemicum*-plastids by the pollen tube takes place. The seedlings were, as expected, less spotted than those of the reciprocal combination (Fig. 9—15).

In all bastards the cotyledon type of *bohemicum* dominated, but in other respects the individuals were typical *deprehensum*-plants (Fig. 1—2). The anthers were sterile. Seeds are not developed by back crossing with the parent types.

The facts respecting our checkered plants are in accordance with the results of RENNER obtained in *Oenothera* species. He has demon-

strated that the plastids of one of the parent plants do not develop normally in cells with a special constitution of the bastard nuclei.

Against the hypothesis of a mixing of two types of plastids by the fertilization of the egg and a subsequent separation during the cell divisions, some important objections have recently been made by CORRENS and NOACK. Considering the various types of inheritance of spotting in plants, I believe that the transmission of plastids may at least for the time being stand as a working hypothesis. It is, however, necessary to investigate whether normal and »sick» chromatophores more often occur in the same cells than hitherto ascertained.

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ZUR ZYTOLOGIE DER GATTUNG GODETIA

VON *ARTUR HÅKANSSON*
LUND

DAS Material für die vorliegende Untersuchung wurde bei dem leider jüngst verstorbenen Genetiker Dr. HANS RASMUSON, Landskrona, gesammelt. Dieser Forscher hat ausgedehnte Studien über die Gattung *Godetia* gemacht (RASMUSON 1921); weil aber in seinen Artkreuzungen zwischen *G. amoena* LILJA und *G. Whitneyi* T. MOORE interessante Sterilitätserscheinungen auftraten, beschloss er, seine genetischen Untersuchungen durch zytologische zu komplettieren. Im letzten Sommer fixierten wir zusammen Blütenknospen von den genannten zwei Arten, von *G. Bottae* und *G. lepida* und ausserdem von dem Bastard *amoena* × *Whitneyi*. Später im Sommer fixierte Dr. RASMUSON reichlich Material von verschiedenen Bastardpflanzen, aber diese Fixierungen scheinen verloren gegangen zu sein. Die ersten Fixierungen hatte ich indessen eingebettet, und konnte die meiotischen Kernteilungen in den PMZ-n [1] an den vier Arten studieren. Von dem Bastarde hatte ich nur ein paar Pflanzen fixiert, die Sterilitätserscheinungen müssen also auf eine eingehendere zytologische Untersuchung harren.

Als Fixierungsmittel wurde meist CARNOYS Alkohol-Eisessig verwendet, aber auch die Lösung von ZENKER. Die Figuren wurden in Arbeitstischhöhe gezeichnet und beim Druck auf $^2/_3$ verkleinert. Die Figuren wurden in der Regel mit LEITZ Ölim. $^1/_{12}$ und Komp. ok. 12 gezeichnet, Fig. 35, 36, 38, 52, 53, 55, 57—60, 62—64 mit Komp. ok. 6.

Die Chromosomenzahl der untersuchten Arten. Bei *Godetia amoena* und *Whitneyi* ist die haploide Chromosomenzahl sieben (siehe unten). *G. lepida* hatte eine weit grössere Zahl, nämlich 21, die Chromosomen dieser Art sind kleiner als die der vorigen. Wie bei *Oenothera* ist also die Grundzahl der Gattung 7; *lepida* ist eine hexaploide Art. Dass die *lepida*-Chromosomen kleiner sind, beruht wohl, wie HEILBORN (1924, S. 173) betreffs der geringeren Chromosomengrösse der vielchromo-

[1] PMZ = Pollenmutterzelle; EMZ = Embryosackmutterzelle.

somigen Formen der Gattung *Carex* (und *Primula*) ausführt, »that there is a limit in the cells' capacity of producing chromatin, which causes the decrease in chromosome size». *G. Bottae* hatte dagegen neun Chromosomen, die grösser als die der anderen Arten waren. Durch weitere Untersuchungen kann man vielleicht höherchromosomige Glieder einer 9er Reihe finden und die verwandtschaftlichen Verhältnisse innerhalb der Gattung auf Grund der Chromosomenzahlen diskutieren. Bei den bisher untersuchten *Onagraceen*-Gattungen kommt, wie erwähnt, bei *Oenothera* die Grundzahl 7, bei *Fuchsia* (WARTH 1923) und der untersuchten *Lopezia* (TÄCKHOLM 1914) 11 vor, und schliesslich haben die fünf untersuchten *Epilobium*-Arten alle 18 Chromosomen (SCHWEMMLE 1924 a, HÅKANSSON 1924).

Die Tapetenzellen. Die Kerne der Tapetenzellen werden durch eine mitotische Teilung während der Zeit, da die Kerne der PMZ-n sich in späten Synapsis befinden geteilt. Die meisten älteren Tapetenzellen haben daher zwei, seltener mehr Kerne, die chromatinreich sind. Oft kamen Kernteilungen auch später vor, dann wurde bisweilen eine vermehrte Chromosomenzahl in den Mitosen beobachtet, mehrmals 28, ja, beim Bastard bis 56 statt 14. Hyperchromosomige Tapetenzellen wurden bei vielen Pflanzen gefunden, z. B. bei *Fuchsia* (BONNET 1912, S. 658). Bei dem Bastard kamen bisweilen hie und da im Tapetenschicht grosse Zellen vor, die gigantische Kerne hatten. In Fig. 64, S. 270 wird gezeigt, wie der Kern einer derartigen hypertrophierten Zelle mit dem grossen Kern einer benachbarten Zelle zusammenschmelzt. Die Tapetenzellen wurden aufgelöst ohne ein Periplasmodium zu bilden, höchstens fliesst ein wenig Zytoplasma zwischen den peripher liegenden Pollenkörnern des Antherenfaches hinein.

Die Prophase der heterotypischen Kernteilung. Die Prophase wurde in den Kernen der PMZ-n der beiden Arten *amoena* und *Bottae* studiert um über die Entstehung der Doppelchromosomen Klarheit zu gewinnen. Aus den Beobachtungen über die präsynaptische Phase kann man wenig Schlüsse auf den Verlauf der Chromosomenkonjugation ziehen, weil die Kerne benachbarter PMZ-n ein sehr verschiedenes Aussehen haben, was möglicherweise auf verschiedenen Gehalt an Chromatin beruht, und auch, wie es schien, weniger gut fixiert waren. Im Anfang der Prophase beobachtet man Chromatinkörner von variierender Grösse, Anzahl und Lage (Fig. 1). Die Körner liegen in den Knoten eines engmaschigen Netzes, das aus feinen, in den Präparaten weniger gefärbten Fäden bestand. Ausserdem hatte der Kern stets mehrere Nukleolen, von denen jedoch nur einer bedeutendere Grösse hatte.

Später ist das Chromatin reichlicher vorhanden, tritt in verschieden grossen Klumpen und Fäden auf. Diese sind bald sehr oft gepaart und immer durch dünnere Fäden mit einander zu einem weitmaschigeren Netz verbunden; offenbar sind viele Querverbindungen aufgelöst (Fig. 2). Ich glaube nicht, dass die Paarung eine »chance parallelism» ist, die bei der Verkürzung des Kernnetzes entstand, wie sie nach CLELAND (1922) bei *Oenothera* zu deuten ist. Dagegen kann man nicht entscheiden, ob es eine Paarung von homologen Chromosomen im Sinne

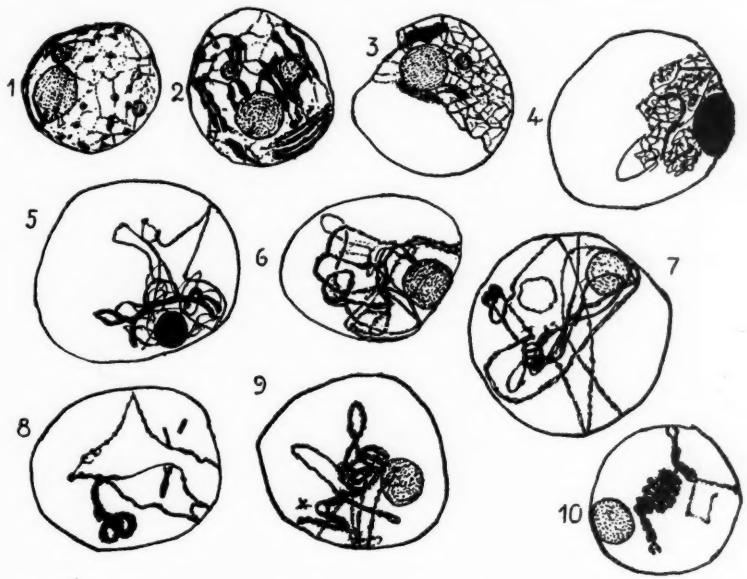

Fig. 1—3. *G. Bottae*, Präsynapsis. Fig. 4—10. *G. amoena;* 4: Synapsis; 5: Späte Synapsis; 6: Der Spiremfaden wird entfaltet; 7—8: Spirem; 9—10: Kontraktion des Spirems.

einer Parasynapsis, oder ein Zusammenkommen von Längshälften von Chromosomen ist, die in der letzten Telophase der Länge nach gespalten wurden (vergl. DIGBY 1919). Das Chromatin zieht sich von einem Teil der Kernmembran zurück und sammelt sich an den Nukleolus (Fig. 3). Die Maschen des Netzes sind infolge der Kontraktion kleiner und eine gleichmässigere Verteilung des Chromatins erfolgt und der Synapsisknäuel ist aus sehr feinen Fäden gebildet, zwischen denen zahlreiche Anastomosen vorkommen (Fig. 3 und 4). Der Kern nimmt im Anfang

der Synapsis bedeutend an Grösse zu. Jetzt kommt nur ein einziger Nukleolus im Kern vor, der eine periphere Lage eingenommen hat. Bisweilen, aber nicht immer, hat er eine abgeplattete Form und liegt dicht an die Kernmembran gedrückt.

Die Veränderungen, die während dem lang andauernden Synapsisstadium vorsichgehen, sind sehr schwierig zu klären. Wenn wir einen Kern am Anfang der Synapsis (Fig. 4) mit einem am Ende derselben vergleichen (Fig. 5), sehen wir, dass der Synapsisknäuel anders aussieht. Die zahlreichen feinen Querverbindungen sind meist aufgelöst, und statt des Netzwerkes haben wir offenbar einen stark gefalteten Kernfaden. Einige nahe den Nukleolus liegenden Fäden sind dicker als die anderen (s. auch Fig. 6). Bei *Oenothera Franciscana* und *Fr. sulfurea* wurde ähnliches von CLELAND (1922, 1924 a) beobachtet, und er deutet die Erscheinung so, dass Chromatinsubstanz vom Nukleolus zum Fadenknäuel abfliesst und dort verteilt wird. Ich wage es nicht seiner Auffassung beizupflichten. Wann und wie die Verschmelzung der in Präsynapsis gepaarten Fäden erfolgt, die wie die spätere Entwicklung zeigt jetzt stattgefunden haben muss, wurde nicht beobachtet, was ja mit Rücksicht auf die grosse Dichte des Synapsisknäuels erklärlich ist.

Am Ende der Synapsis gehen von dem am Nukleolus liegenden Knäuel immer zahlreichere Schleifen des Spiremfadens aus, die oft die Kernmembran tangieren (Fig. 5). Fig. 6 zeigt einen Kern, bei dem sich der Spiremfaden über den ganzen Kernraum verbreitet. Wenn auch hie und da Querverbindungen vorzukommen scheinen, so ist es doch offenbar, dass das Chromatin meist einen einzigen Faden bildet. Er ist nicht von gleichmässiger Dicke, gröbere Fadenteile sind überall zu beobachten, insbesonders liegt ein dickes Fadenende am Nukleolus. In Fig. 7 ist der Spiremfaden mehr entfaltet und bildet mehrere grosse Schleifen. Jetzt tritt eine deutliche Chromomerenstruktur in den dickeren Fädenteilen auf. Die Chromomeren bilden eine einzige Reihe und scheinen nirgends gespalten zu sein. Den Spiremfaden kann man oft in seiner ganzen Länge verfolgen; in Kernen, die nicht durch den Messer zerlegt wurden, kann man keine »freie Enden» beobachten, und er ist also kontinuierlich wie bei den *Oenotheren.*

Die folgende Entwicklung wird dadurch gekennzeichnet, dass eine Verkürzung und Verdickung des Spirems stattfindet. Im Zentrum des Spirems sind die Fäden während der Kontraktion oft besonders dick und um einander zu einem kleinen Knäuel gewickelt. Dieser Knäuel kann schon in Fig. 7 beobachtet werden, und vielfach dürfte er seit der

Synapsis bestehen. Die an der Kernmembran liegenden Fädenteile sind am Anfang der Kontraktion besonders dünn, als ob sie fest an der Membran hafteten und jetzt ausgezogen wurden (Fig. 8; der Kern ist nur angeschnitten). Die Schleifen werden infolge der Verkürzung des Spiremfadens immer kleiner (Fig. 9 und 11). Das Spirem sammelt sich meist in der Mitte des Kerns, aber selten tritt eine so grosse Kontraktion des Fadens wie in Fig. 26 abgebildet ist ein. Auch in Fig. 10 ist eine sehr starke Zusammenballung sichtbar. Bei *Oenothera Fran-*

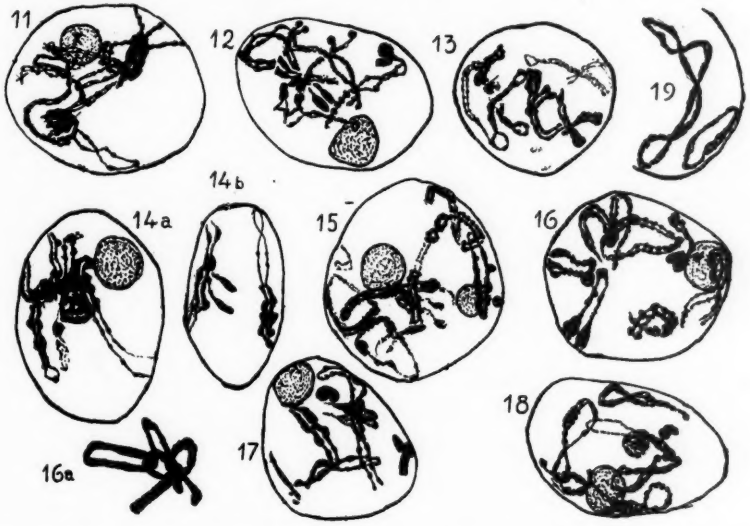

Fig. 13, 16 a, 19: *G. Bottae*, die übrigen *G. amoena*; 11: Beginnende Spaltung und Segmentierung des Spirems; 12—15, 17 (14 a und b beziehen sich auf denselben Kern): Weitere Spaltung und Verdickung der Segmente; 16, 18: Strepsinema oder frühe Diakinese. Die zweite Spaltung tritt auf. 16 a, 19: Strepsinemachromosomen.

ciscana und *Fr. sulfurea,* wo der Spiremfaden sich bisher wie bei *Godetia* verhielt (CLELAND), wurde er immer sehr stark kontrahiert. Bei *Godetia* trat dagegen eine Segmentierung des Fadens ein, während er noch ziemlich dünn war. Die Segmente kamen, wenn das Zerfallen des Fadens vollständig war, in der haploiden Zahl vor (Fig. 12 u. f.), die Segmentierung ist aber oft nicht simultan, und mehrere der Segmente hängen oft lange zusammen (Fig. 15). Auch tritt, was bei den erwähnten *Oenotheren* nach CLELAND sehr selten geschieht, eine Längsspaltung auf. Im unsegmentierten Faden ist diese nur dadurch an-

gedeutet, das hie und da zwei Chromomeren mehr oder weniger weit von einander getrennt liegen, wo früher offenbar eine einzige grössere Chromomere lag. In Fig. 9 und 11 hat somit Spaltung bei mit x bezeichneten Stellen stattgefunden; in Fig. 11, wo das Spirem teilweise segmentiert ist, sind in einem Segmente die Spalthälften weiter von einander getrennt und um einander gedreht. Die Dünnheit der Spalthälften zeigt deutlich, dass eine Spaltung stattfand und dass das

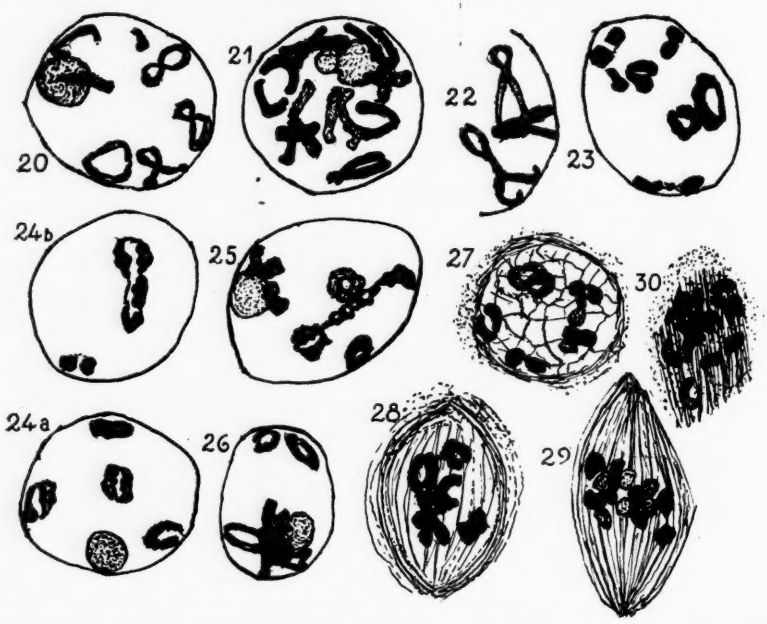

Fig. 20—22, 26: *G. Bottae*, Fig. 30: *G. Whitneyi*, die übrigen *G. amoena*. 20—22: Strepsinema oder frühe Diakinese; 23—25: Diakinese (24 a und b beziehen sich auf denselben Kern); 26: Abnorme Kontraktion; 27: Späte Diakinese; 28: Doppelchromosomen auf der Kernspindel; 29: Heterotypische Metaphase; 30: Anaphase (quergeschnitten).

fragliche Segment nicht eine Spiremschleife ist, deren Schenkel sich näherten. In Fig. 12 ist die Segmentierung beinahe vollständig, und die Längshälften sind in verschiedener Weise auseinandergewichen, so dass die Segmente ein sehr verschiedenes Aussehen haben. Fig. 13 zeigt einen ähnlichen Kern von *G. Bottae*, der jedoch durch das Messer zerlegt wurde; die Segmente sind somit nicht in ihrer ganzer Länge sichtbar.

Ist also unzweifelhaft die Doppelheit der Segmente in Fig. 12 durch Spaltung entstanden und nicht durch Zusammenlegen von Schleifenschenkeln (»conjunction»), so bleibt jetzt zu entscheiden, ob die Doppelchromosomen durch Umbiegung dieser Segmente gebildet werden (also Telosynapsis), oder ob sie durch direkte Verkürzung der Segmente entstehen (Parasynapsis). Trennt die erwähnte Spalte die Längshälften univalenter Chromosomen (»fission» im Sinne DIGBY 1919), oder trennt sie Chromosomen, die in Präsynapsis und Synapsis konjugierten? Die Entscheidung wird dadurch erschwert, dass bei *G. amoena* in der Regel, bei *G. Bottae* ziemlich oft eine Spalte in den Chromosomen während der Diakinese zu sehen ist (Fig. 24), eine Spalte die noch früher auftrat (Fig. 16), die in der Metaphase verschwunden ist (Fig. 29), um schliesslich in der späten Anaphase oder Telophase aufs neue aufzutreten. Das ist die homotypische Spaltung (»fission») und man könnte meinen, die frühere Spaltung, die in Fig. 12 und 14 sichtbar ist, sei dieselbe wie die in den Chromosomen in Fig. 16 und 18. Demgegenüber bin ich überzeugt, dass die letztgenannte eine neue Spaltung ist, denn es gibt eine grosse Verschiedenheit der Spaltungen. In der ersten gehen die Hälften stellenweise weit auseinander, ösenähnliche Bildungen entstehen oft am Ende oder in der Mitte der Segmente, und wie GRÉGOIRE betreffs *Lilium* hervorhob (1907, S. 379—380), deutet ein so grosses Auseinanderweichen darauf, »les deux apparentes 'moitiés longitudinales' ne sont pas des vraies moitiés provenant d'un clivage réel, mais deux filaments indépendants accolés». Die zweite Längsspaltung erhält dagegen nie grössere Breite, die Spalthälften liegen immer dicht bei einander.

Eine Verdickung und Verkürzung der Segmente erfolgt (Fig. 14, 15, 17), die wie gewöhnlich von Umbiegungen der Segmente und Drehungen der gepaarten Chromosomen um einander begleitet ist (Fig. 18—20). Strepsinemachromosomen in verschiedener Verkürzung zeigen Fig. 16, 18—22, sie ähneln sehr den Segmenten in den früheren Phasen und es dürfte zweifellos sein, dass sie durch direkte Verkürzung der letzteren entstehen, Parasynapsis also bei *Godetia* vorkommt. Bei den *Oenotheren* ist dagegen nach den meisten Forschern ein univalentes Spirem vorhanden, worin die Chromosomen end-to-end liegen und Doppelchromosomen werden dort durch Annähern benachbarter Schenkel von Schleifen gebildet (CLELAND). Im Gegensatz dazu fand jedoch BOEDYN neulich (1924) Parasynapsis wie bei *Godetia* indem Fäden in der Synapsis konjugierten, und in einer späteren Phase von dem Spirem abgetrennt sich spalteten.

Die Paarung der Chromosomen war während der Diakinese (Fig. 23—25) gut. In Fig. 21 sehen wir die noch nicht maximal verkürzten neun *Bottae*-Doppelchromosomen. Bei den *Oenotheren* ist bekanntlich die Paarung meist sehr schlecht, bei *grandiflora* kommen aber sieben Doppelchromosomen vor, die wie bei *Godetia* oft der Fall ist, wie Ringe aussehen (DAVIS 1909). Bei *Oe. Hookeri* (SCHWEMMLE 1924 a), *deserens, blandina* (CLELAND 1924 b) gibt es auch sieben Gemine, bei *Franciscana* (CLELAND 1922) fünf nebst einem Ring von vier, wie er einmal bei *G. amoena* (Fig. 24) beobachtet wurde. Nach CLELAND soll die Paarung homozygotische *Oenotheren* kennzeichnen, nach GATES (1923) ist sie jedoch auch bei dem 15-chromosomigen Bastard *rubricalyx* × *Hewitti* gut, indem dort fünf Gemine auftreten. Fig. 26 zeigt wie sich die meisten Doppelchromosomen in dem abnorm kontrahierten Spirem bilden. Fig. 16 a zeigte eine Verkettung von wohl in ähnlicher Weise entstandenen Chromosomen. Zwei Nukleolen treten in Strepsinema und später in Diakinese auf.

Der weitere Verlauf der Reduktionsteilung bei den vier Arten. Am Ende der Diakinese tritt ein Netzwerk von feinen Fäden im Kerne auf, während die Kernmembran gleichzeitig weniger deutlich wird. Schon etwas früher hat sich aber eine Zone von dichterem Zytoplasma, in welchem feine Fäden zu sehen sind, um den Diakinesenkern gesammelt (Fig. 27). Die heterotypische Kernspindel ist wie gewöhnlich anfangs multipolar, die Chromosomen liegen erst zerstreut (Fig. 28) und ordnen sich, wenn die Spindel bipolar wird, zu einer Metaphasenplatte, in der die Chromosomen nach den Polen gerichtet sind (Fig. 29). Während der Anaphase haben die Chromosomen wie bei den *Oenotheren* eine halbmondförmige Form, wie aus Fig. 30 ersichtlich ist, wo die beiden Chromosomengruppen bei zwei verschiedenen Einstellungen der Mikrometerschraube hervortraten. Die Chromosomen gehen bisweilen nicht gleichzeitig auseinander, bisweilen lagen die gepaarten Chromosomen früh von einander getrennt.

Bei *G. Bottae* sind die Chromosomen grösser als bei *amoena* und *Whitneyi,* zwischen den letzteren Arten kommen wahrscheinlich geringe Verschiedenheiten vor. Bei *lepida* waren sie, wie erwähnt, kleiner. Bei der letztgenannten Art beobachtete ich nur homotypische Teilungen und übrigens nur wenige solche. In Fig. 39 sehen wir eine homotypische Metaphase mit wie es scheint, 21 Chromosomen, in Fig. 40 einen soeben gebildete Tetradenkern mit 21 Chromosomen nebst als Band auftretende Nukleolarsubstanz. Ich beobachtete in der Nuzellusepidermis der Samenanlagen somatische Kernplatten, wo die Chromosomen gut

von einander getrennt lagen. Etwa 42 Chromosomen wurden gezählt (Fig. 37, zwei gebogene Chromosomen sind zweimal geschnitten). Zweifellos ist also die haploide Chromosomenzahl 21.

In der Telophase der heterotypischen Teilung tritt eine Spaltung der Chromosomen auf, die in der Interkinese wie X aussehen (Fig. 31). In der Regel werden sie noch mehr geteilt. Die homotypischen Kern-

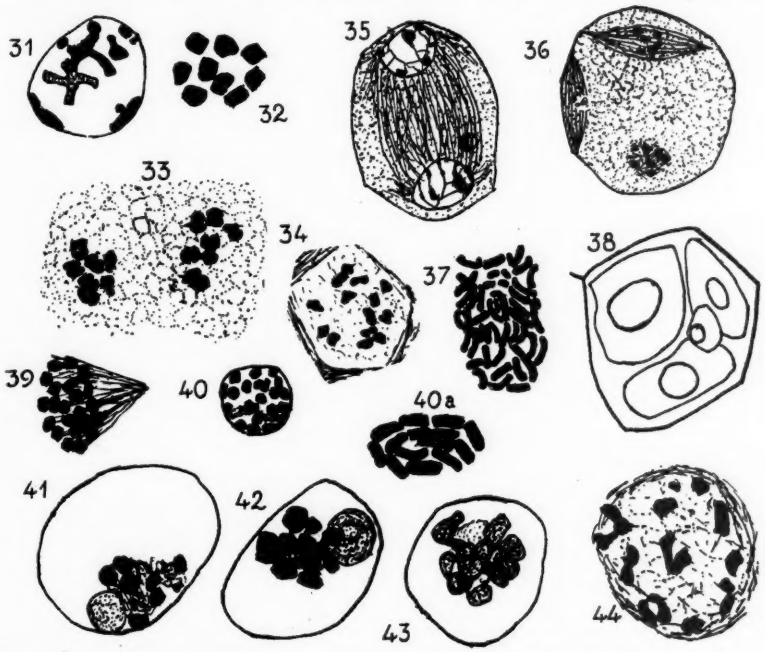

Fig. 31: *G. Whitneyi*, Interkinese; 32: *G. Bottae*, Homotypische Kernplatte; 33: *G. amoena*, Homotypische Kernplatten; 34: *G. amoena*, Homotypische Anaphase; 35: *G. Whitneyi*, Interkinese; 36: *G. Whitneyi*, Homotypische Kernspindeln; 37: *G. lepida*, Somatische Kernplatte; 38: *G. Whitneyi*, Pollentetrade; 39: *G. lepida*, Homotypische Metaphase; 40: *G. lepida*, Junger Tetradenkern; 40 a—44: *G. amoena* × *Whitneyi*; 40 a: Somatische Kernplatte; 41—43: Heterotypische Prophase; 44: Diakinese.

spindeln werden multipolar angelegt, bald aber werden sie bipolar. Die Chromosomen sind in der Metaphase gespalten (Fig. 33), bei *Whitneyi* waren die Hälften bisweilen von einander getrennt, und die Kernplatte hatte dann eine vermehrte Chromosomenzahl. Eine homotypische Anaphase zeigt Fig. 34. Bei *Whitneyi* wurden einige Unregelmässigkeiten bei der Reduktionsteilung bisweilen beobachtet. Verspätete

Chromosomen bildeten Kleinkerne (Fig. 35), die später geteilt wurden (Fig. 36). Beim Bastarde sind ähnliche Störungen weit gewöhnlicher. Eine abnorme Pollentetrade mit drei grossen und einer kleinen Zelle zeigt Fig. 38.

Die Pollenkörner bei *amoena* und *Whitneyi* sind dreieckig wie bei den diploiden *Oenotheren,* nur selten wurden viereckige beobachtet. Bei *lepida* kamen dagegen viereckige Pollenkörner neben den dreieckigen zahlreich vor. Die Pollenkörner hatten bei dieser Art bedeutendere Grösse. Gereifte Pollenkörner wurden bei *amoena* gesehen. Sie waren voll von spindelförmigen Stärkekörner. Der vegetative Kern des Pollenkorns war oft gelappt.

Die Pollenentwicklung beim Bastard. Aus Gründen, die einleitungsweise erwähnt wurden, habe ich nur Blütenknospen einiger Pflanzen des Bastardes *G. amoena* × *Whitneyi* untersucht. Beobachtungen wurden auch über die Samenentwicklung gemacht. Die diploide Chromosomenzahl wurde in Kernplatten des sterilen Gewebes des Anthers auf 14 bestimmt (Fig. 40 *a*).

Die heterotypische Prophase konnte leider wenig studiert werden, Kerne mit stark zusammengeballtem Synapsisknäuel, oder mit einem groben grössenteils eingerollten Spiremfaden wurden oft beobachtet, die folgenden Stadien fehlten aber beinahe vollständig. Mehrere Kerne hatten die Chromosomen gebildet, die dicht beisammen lagen (Fig. 42). Man könnte meinen, dass sie wie bei *G. amoena* gebildet, dann aber infolge Degeneration zusammengeballt wurden. Möglicherweise wurden sie aber in dem abnorm lang andauernden Synapsisknäuel gebildet, wie aus Fig. 41 vielleicht hervorgeht. PMZ-n wurden beobachtet, worin diese Chromosomenmasse nach Auflösung der Kernmembran frei im Zytoplasma lagen.

Die Chromosomen haben beim Bastard eine viel grössere Neigung zur Kettenbildung als bei *amoena.* Fig. 43 zeigt einen Kern, worin sämtliche Chromosomen eine einzige Kette bilden, so dass ein *Oenotheren*-ähnliches Bild entsteht. Ähnliches wurde auch in einem EMZ-Kern beobachtet (Fig. 61). Ein solche Verklebung kommt vielleicht regelmässig vor, was doch erst nach Untersuchung von mehr Material entschieden werden kann. Nach Auflösung der Kernmembran liegen die Chromosomen jedoch von einander isoliert. In der Metaphase, die sehr oft, und in der späten Diakinese, die einige Male beobachtet wurde, treten gepaarte und ungepaarte Chromosomen auf, meist gab es jedoch nur zwei ungepaarte nebst sechs Paare. Fig. 44 zeigt einen Kern mit nur vier Doppelchromosomen, sechs Einzelchro-

mosomen liegen zerstreut, daneben zwei kleinere chromatische Körper, die wahrscheinlich Reste des Nukleolus, möglicherweise Chromosomenfragmente sind. In Fig. 45 haben fünf der Doppelchromosomen eine charakteristische Stäbchenform, die man immer in den Metaphasen beobachten kann, wo nie mehr als fünf aber oft weniger Doppelchromosomen dieses Aussehen besitzen. Die Figur zeigt noch ein Doppelchromosom und zwei Ungepaarte. Die Stäbchenform kommt dadurch zustande, dass die Chromosomen eines Paares am einen Ende fest verklebt sind, während sie am anderen durch den Zug der Spindelfasern stark ausspreizen.

Die Chromosomen werden wohl in der Regel zu einer regelmässigen Kernplatte geordnet. Dies scheint jedoch nicht immer zu geschehen. In der in Fig. 46 abgebildeten Kernspindel lagen wohl die Chromosomen nie streng nebeneinander. Die mit 1 bezeichneten sind die Ungepaarten. In Fig. 48 sehen wir eine schief geschnittene Anaphase, wo die Ungepaarten (1) in der Peripherie der Kernplatte liegen. In zwei Doppelchromosomen (2 u. 5) liegen die Chromosomen beisammen, in den anderen sind sie getrennt. Sehr oft kommt es vor, dass ein Chromosom den einen Pol der Kernspindel erreicht hat, während die anderen noch beim Äquator liegen (siehe Fig. 49). Nicht selten wandern zwei Chromosomen früher als die anderen, entweder nach demselben oder verschiedenen Polen. In Fig. 49 haben mehrere Chromosomen schon die telophasige Teilung durchgemacht. Oft geschieht eine Querteilung von Chromosomen, indem von den stabförmigen Doppelchromosomen, die oft einige durch dünnere Partien getrennte Verdickungen zeigen (Fig. 47), der verdickte Endteil abgetrennt wird. Schliesslich liegen in der heterotypischen Metaphase bisweilen Chromosomen oder Chromosomenfragmente frei im Zytoplasma (Fig. 47). Wie sie ausserhalb des Wirkungskreises der Kernspindel gelangten, wurde nicht ermittelt.

Während der Anaphase sind die Chromosomen oft über die ganze Kernspindel zerstreut. Chromosomen werden sehr oft in so hohem Grade verspätet, dass sie nicht mit den Dyadenkernen einverleibt werden. Diese »lagging chromosomes» erleiden dieselben Veränderungen wie die anderen. Sie werden also längs- und quergeteilt (Fig. 50), von einer Kernmembran umgeben, während sich zwischen Chromatin und Membran eine Kernvakuole bildet (Fig. 53). Selbst um ein Chromosomenfragment kann sich eine Kernmembran bilden (siehe Fig. 58 betreffs der homotypischen Teilung). An den Polen der Kernspindel liegen die Chromosomen oft ziemlich zerstreut. Dadurch entstehen

bisweilen gelappte Dyadenkerne (Fig. 52) oder Kleinkerne, die im Kontakt mit dem Dyadenkern liegen und mit dem letzteren verschmelzen können (Fig. 51). Bisweilen verbleibt ein Strang von Chromatin in der Telophase auf der Kernspindel (vergl. Fig. 56). Bisweilen kommen sehr grosse Dyadenkerne vor, die wie es scheint, mehr als sieben Chromosomen haben (Fig. 51, 52). Fig. 50 zeigt die Eigentümlichkeit,

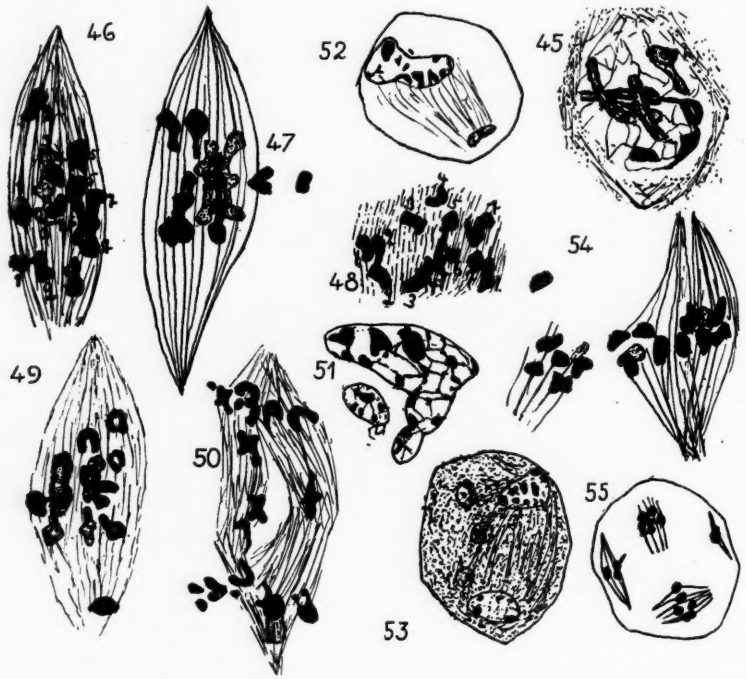

Fig. 45—55: *G. amoena* × *Whitneyi*; 45: Diakinese; 46—50: Heterotypische Meta- und Anaphase; 51: Interkinesenkern; 52—53: Interkinese; 54—55: Homotypische Kernspindeln.

dass die heterotypische Kernspindel längs der Mitte geteilt ist; eine starke Verbreitung der Kernspindel scheint dadurch einzutreten, und »lagging chromosomes» werden wie es scheint bis an die Kernmembran geführt, was das Vorkommen von Kleinkernen dort, wie man sie oft beobachten kann, erklärt.

Während der homotypischen Teilungen werden auch die Kleinkerne geteilt. Doch wurden nie mehr als vier Kernspindeln beobachtet

(Fig. 55), trotzdem bisweilen mehr als vier Kerne nach der heterotypischen Teilung gebildet wurden. Offenbar werden oft die Chromosomen zweier Kernen mit derselben Kernspindel einverleibt (Fig. 54). Man kann oft eine Chromatinbrücke zwischen zwei Chromosomen, die in verschiedenen Kernspindeln liegen, beobachten (Fig. 55—57). Es scheint, als ob ein Kleinkern bisweilen in den Wirkungskreis zweier Kernspindeln kommt und ihr Chromosom zwischen den beiden aufgeteilt wird, was zu den erwähnten Erscheinungen Anlass gibt. Eigentümlich ist Fig. 55, in der zwei Chromosomen in ähnlicher Weise geteilt sind. In der homotypischen Metaphase liegen die Chromosomen oft früh geteilt. Ähnliche Unregelmässigkeiten wie in der heterotypischen Teilung waren gewöhnlich. »Lagging chromosomes», Bildung von Kleinkernen usw. wurde oft beobachtet (siehe Fig. 56 u. 58). Nach abgeschlossenen Kernteilungen hat die PMZ also oft mehr als vier Tetradenkerne (Fig. 59). Sie haben verschiedene Grösse, was auf verschiedener Chromosomenzahl beruht. Die neben den grösseren Tetradenkernen liegenden Kleinkerne verschmelzen oft mit den erstgenannten (Fig. 58). Ich will schliesslich erwähnen, dass zahlreiche PMZ-n beobachtet wurden, wo sämtliche vier Chromosomengruppen in der homotypischen Ana- oder Telophase sieben Chromosomen hatten, wo also die allotypischen Kernteilungen vollständig normal verlaufen sind. Normalchromosomige Pollenkörner werden also sehr oft gebildet.

Die Zellteilung geschieht ohne Zweifel durch »furrowing», die jedoch schwer zu beobachten und zu zeichnen ist. In den Spindelfasern treten nie Zellplatten auf, ja, jene nehmen an Anzahl gleich vor der Zellteilung ab. Von der Peripherie gehen offenbar sehr rasch zarte Furchen durch die PMZ, die auf diese Weise in Pollenzellen zerlegt wird. Bald erscheint der etwas erweiterte äusserste Teil der Furche noch weiter (Fig. 60), und eine mit Lichtgrün färbbare Substanz, die eine Fortsetzung der Wand der PMZ ist, ist in der Furche sichtbar. Nach CLELAND kommt »furrowing» bei *Oenothera Franciscana* und *Fr. sulfurea* vor, die durch sehr feine Furchen erfolgt. Pollentetraden mit bis acht Zellen wurden beobachtet. Viele Pollenzellen sind sehr klein, nämlich die, die um kleine Kerne gebildet werden. In der ältesten untersuchten Blütenknospe hatten die Pollenkörner offenbar volle Grösse erlangt. Die meisten waren so gross wie bei *G. Whitneyi*, ihre Wand hatte normale Dicke, wenn auch die »Zwischenkörper» ein wenig abnorm entwickelt schienen; ihr Protoplast war dagegen klein und war mit dem Kern in Degeneration, was sich in einer starken Chromo-

philie äusserte. Das Wachstum der Wand geschieht ja unter Mitwirkung der Tapetenschicht, die beim Bastard gut entwickelt war.

Der untersuchte *Godetia*-Bastard hatte zwar gleichchromosomige Eltern, doch traten ungepaarte Chromosomen in der Diakinese und Metaphase auf, weil offenbar die Affinität zwischen den Chromosomen

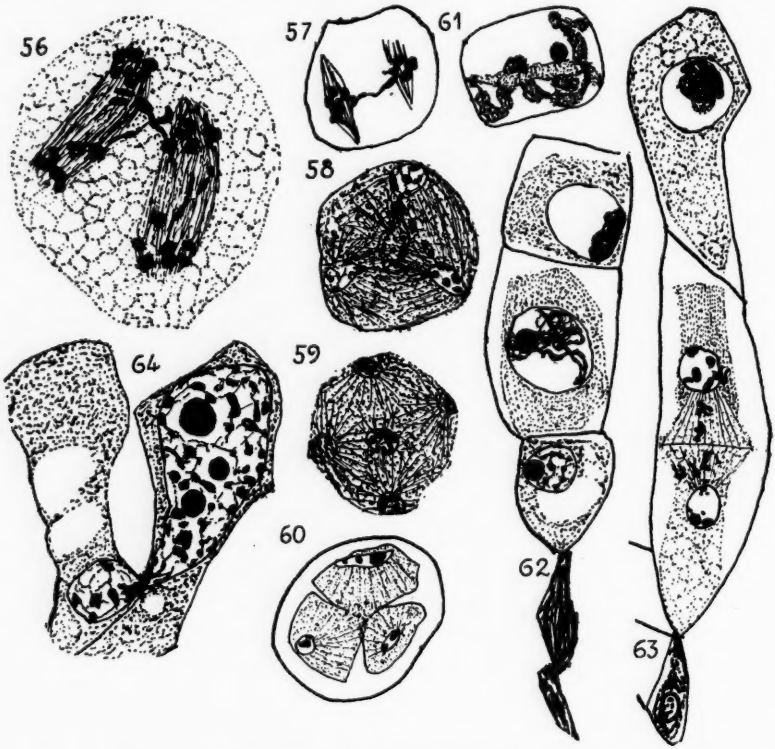

Fig. 56—64: *G. amoena* × *Whitneyi*. 56: Homotypische Anaphase; 57: Homotypische Metaphase; 58—59: Pollentetraden; 60: Pollentetrade, Zellbildung; 61: EMZ-Kern in Prophase; 62: Zwei EMZ-n und persistierende Makrospore; 63: EMZ und Dyadenzellen; 64: Zwei hypertrophierte Tapetenzellen, Kernübertritt und -verschmelzung.

eines Paares so schwach war, dass sie in der Regel von einander getrennt lagen. Bekanntlich hat man bei anderen Bastarden gleichchromosomigen Pflanzen eine noch schwächere Affinität gefunden, so neulich in *Raphanus sativus* × *Brassica oleracea* (beide n = 9), in deren PMZ-n 18 ungepaarte Chromosomen zu sehen sind (KARPECHENKO 1924, merkwürdiger-

weise traten hier in der einzigen beobachteten Metaphase in der EMZ 9 Paare auf). Zahlreiche Unregelmässigkeiten, die Veranlassung zur Bildung von kleineren und grösseren Pollenkörnern mit weniger als sieben Chromosomen geben, wurden oben beschrieben. Betreffs der Fertilität des Pollens sagt RASMUSON (1921, S. 262): »Das Pollen war spärlich und immer sehr schlecht und in einer Kreuzung (I) wahrscheinlich völlig untauglich.» Die Pollenkörner mit weniger als sieben Chromosomen sterben wohl zuerst, aber offenbar werden nicht alle mit sieben normal entwickelt. Möglich ist, dass ein Bastardpollenkorn fertil wird, wenn es einen vollständigen Satz von entweder sieben *amoena*-Chromosomen oder sieben *Whitneyi*-Chromosomen bekommt. Das kann vielleicht durch ein eingehenderes Studium der Vererbungserscheinungen, Fertilität und Chromosomenverhältnisse einer grösseren Anzahl verschiedener Bastardpflanzen gezeigt werden. In der erwähnten Kreuzung I traten vielleicht noch stärkere Störungen in der Chromosomendistribuierung auf.

Bekanntlich sind die Chromosomen der *Oenotheren* in der Diakinese in Ketten oder Ringe geordnet. Nach CLELAND (1922, 1924 a, 1924 b) ist dies eine sehr regelmässige Erscheinung. Die Diakinesenchromosomen treten teils als Paare auf, teils als einen mehrere Chromosomen umfassenden Ring, und die verschiedenen *Oenotheren* haben eine bestimmte Chromosomenanordnung, z. B. *Lamarckiana* ein Paar und einen Ring von 12 Chromosomen, *Franciscana* 5 Paare und einen von vier usw. (elf Formen wurden bisher untersucht, s. CLELAND 1924 b). Ferner liegen die ringbildenden Chromosomen in bestimmter Weise orientiert, und in der heterotypischen Anaphase geht jeder zweite Chromosom von dem Ringe nach demselben Pol, wodurch es wahrscheinlich wird, dass die dem einen haploiden Satz angehörenden nach dem einen Pol, die zu dem anderen gehörenden nach dem anderen Pol kommen. Eine zytologische Erklärung mancher der Vererbungserscheinungen der *Oenotheren* ist nach CLELAND durch diese Verhältnisse gegeben, so die Koppelung zahlreicher Gene (grosse Genenkomplexe), das Vorkommen von nur zwei Arten Gameten bei vielen *Oenotheren*, auch dass die Chromosomenkomplexe dieser Gameten dieselben sind, die einmal zusammentrafen und die betreffende *Oenothera*-Form bildeten (1924 b). Die Kernchimärentheorie von LOTSY hätte somit eine zytologische Stütze gefunden.

Bei den untersuchten *Godetia*-Arten kamen ähnliche Erscheinungen nicht vor. Nur selten wurden einige verkettete Chromosomenpaare beobachtet. Aber die Vererbungseigentümlichkeiten fehlen auch hier

(RASMUSON 1921). Bei dem Bastard kam dagegen Verkettung von Chromosomen viel öfter vor, so dass einige Male »*Oenotheren*-ähnliche» Bilder zu sehen waren. Falls bei Untersuchung eines reichlicheren Materiales von verschiedenen Bastardpflanzen hervorgeht, dass die Verkettung eine Erscheinung ist, die auch in PMZ-n, wo eine Degeneration ausgeschlossen ist, vorkommt, so ist es klar, dass sie durch die Bastardierung hervorgerufen wird. Dadurch wird es auch wahrscheinlich, dass sie bei den *Oenotheren* durch eine frühere Bastardierung hervorgerufen wird, was nach CLELAND (1924 b) möglich ist. Bei *Epilobium,* wo wie bei *Godetia* Parasynapsis und keine Ringbildung der Chromosomen vorkommt, sind nach den Untersuchungen von LEHMANN, ÅKERMAN u. a. »die Gene . . . nicht in starren Komplexen zusammengehalten» (ÅKERMAN 1921, S. 109).

Die Samenentwicklung beim Bastard. Ich habe wie erwähnt einige Beobachtungen über die Samenentwicklung der untersuchten Bastarde *G. amoena* × *Whitneyi* gemacht. Aus RASMUSON's Versuchen ging hervor, dass einige der Samenanlagen Samen geben können, während die grosse Mehrzahl steril ist (l. c., S. 262).

Die Samenentwicklung der beiden Arten *amoena* und *Whitneyi* wurde von TÄCKHOLM (1915) untersucht, die Embryosackentwicklung ist dort wie bei anderen *Onagraceen.* Bei *amoena* kam nach diesem Forscher nur eine EMZ im Nuzellus vor, bei *Whitneyi* dagegen mehrere, wohl meist fünf, »ihre Zahl übersteigt in der Regel nicht sieben». Die Samenanlagen des Bastardes hatten in der Regel mehrere EMZ-n, meist wurden zwei oder drei beobachtet, aber bisweilen bis fünf, eine geringere Zahl also als bei *Whitneyi.* Die EMZ-n liegen meist in einer Reihe (Fig. 62), und die chalazale ist die grösste und eilt in der Entwicklung voraus. Ihr Kern wurde in verschiedenen Prophasenstadien beobachtet (Fig. 61), in der späteren Diakinese kamen gepaarte und ungepaarte Chromosomen vor. Während der heterotypischen Teilung wurden ähnliche Unregelmässigkeiten wie in den PMZ-n beobachtet. Verspätete Chromosomen lagen auf der Kernspindel, die nicht in die Dyadenkerne gelangten (Fig. 63). Vielleicht degenerierten sie im Zytoplasma, denn Kleinkerne wurden nie beobachtet. Homotypische Kernteilungen wurden beobachtet, aber die drei chalazalen Makrosporen werden anscheinend sehr rasch in eine chromophile Masse verwandelt. Ich weiss nicht, wie oft sich die persistierende Makrospore über das in Fig. 62 abgebildete Stadium entwickelt. Überhaupt erscheint die Samenentwicklung beim Bastard sehr verspätet, als wenn sie nur mit Mühe vor sich ging. Ziemlich alte Ovarien wurden geschnitten, aber nur ein-

mal hatte die fragliche Spore sich so verlängert, dass es deutlich war, dass sie einen normalen Embryosack bilden dürfte. Spätere Entwicklungsstadien wurden nicht untersucht, und ich weiss nicht, wie viele Samenanlagen einen Embryosack entwickeln.

Dies dürften indessen nur ziemlich wenige tun. In den Ovarien waren viele Samenanlagen völlig steril und hatte keine sporogenen Zellen. Die EMZ-n schrumpfen oft, werden stark chromophil und schliesslich verdrängt. Auch wenn die chalazale EMZ geteilt wird, degenerieren oft die Makrosporen, und es schien, als ob der einkernige Embryosack oft in dem in Fig. 62 abgebildeten Stadium degenerierte. Besondere Neigung zur Degeneration hat wohl der Embryosack, wenn er eine andere Chromosomenzahl als sieben enthält. Ähnliche abnorme Samenanlagen wie TÄCKHOLM (1915) bei *Godetia* »*Gloriosa*» (»eine hybridenverdächtige Form») beobachtete, kamen hier nicht vor.

Ein Vergleich mit den zytologischen Verhältnissen in den Samenanlagen verschiedener *Epilobien* ist von Interesse. In dem von mir untersuchten *E. hirsutum* × *montanum* war die Reduktionsteilung normal, ein Embryosack entwickelte sich in der Regel, der auch oft befruchtet wurde. Bei drei untersuchten Rückkreuzungspflanzen entwickelte sich auch ein Embryosack in der Samenanlage, in zwei von diesen Pflanzen wurde er befruchtet und bildete Embryonen, in der dritten degenerierte er dagegen immer, ohne befruchtet zu werden (HÅKANSSON 1924). Der von SCHWEMMLE (1924 b) untersuchte *E. parviflorum* × *roseum* verhielt sich wie die letztgenannte Pflanze: ein vollständiger Embryosack wurde gebildet, der immer degenerierte. In der reziproken Kreuzung *roseum* × *parviflorum* fand SCHWEMMLE eine ganze Stufenreihe von Sterilitätserscheinungen. Eine Form, *curvatum* 2006, verhielt sich offenbar wie *hirsutum* × *montanum* und die erwähnten fertilen Rückkreuzungspflanzen, *curvatum* 2008/2009 wie der hier beschriebene *Godetia*-Bastard, indem nur selten ein fertiler Embryosack entwickelt wurde; *curvatum* 1901 zeigte eine noch stärkere Sterilität, nur selten wurde in der Samenanlage eine EMZ gebildet, die meisten Samenanlagen waren steril.

Lund, Botanisches Institut.

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INNEHÅLL.

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